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THE LARVAL DEVELOPMENT OF *LITORIA BREVIPALMATA* (ANURA:HYLIDAE)

MARION ANSTIS

Anstis, M. 1994 12 01; The larval development of *Litoria brevipalmata* (Anura: Hylidae). *Memoirs of the Queensland Museum* 37(1): 1-4, Brisbane, ISSN 0079-8835.

The tadpole of *L. brevipalmata* is unique amongst Australian hylid frogs of the pond dwelling nektonic type in possessing a median vent tube. The embryo is one of a small number of species so far known to have three pairs of external gills. □ *Anura, Hylidae, Litoria brevipalmata, embryonic and larval development.*

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Litoria brevipalmata Tyler, Martin & Watson, 1972 is the sole member of the *Litoria brevipalmata* species group of Tyler & Davies (1976). A medium-size, ground-dwelling species, it is readily distinguished from congeners by the combination of a rich brown dorsal colour and pale green in the axilla, groin and posterior surface of the thighs.

The type description was based on a series of adult frogs collected at Durimbah Ck near Gosford, NSW, and Byaburra (near Wauchope) NSW, but no information on life history was presented. McDonald (1974) reported its occurrence at Ravensbourne and Crows Nest National Parks in SE Queensland, and the frog was found subsequently at Jimna, 80km north of these localities (Czechura, 1978) and in the Kilcoy Shire (McEvoy et al., 1979). Barker & Grigg (1977) stated that large numbers of males were calling after rain in a flooded paddock near Gosford (late October, 1972), and noted that juveniles were collected during April in wet sclerophyll forest.

Two more recent records are now known from near Woogaroo Ck near Wacol, Brisbane (Nattrass & Ingram, 1993). This is the only published coastal locality so far for the species. However, in the summer of 1993/1994 there have been further records from Marsden, Karawatha, Beerwah and Nambour (G. Ingram, pers. comm.).

The present paper describes the only available embryo and larval material.

MATERIALS AND METHODS

The following description is based on an egg mass from one pair of frogs collected by H.G. Cogger on 29 October, 1972. The pair was taken from beside a permanent pond in a paddock near Ourimbah Ck, Gosford NSW after heavy rain and amplexus occurred in a plastic bag. The eggs were laid during the evening of 30 October. Most embryos died in transit. One was preserved at stage 9, five at stage 17, one at stage 20 (just hatched), one tadpole at

each of stages 37 and 41 and one newly metamorphosed at stage 46. Specimens are lodged in the Australian Museum (AMR118482, AMR118483).

Tadpoles were raised in an outdoor container of pond water experiencing variable water temperatures (16-25°C), and were fed on boiled lettuce. Tadpoles were anaesthetised in Chlorbutol solution, then embryos and tadpoles preserved in Tyler's (1972) Fixative. Specimens were measured with a vernier caliper to 0.01mm, or an ocular micrometer attached to a stereoscopic microscope. The staging system is that of Gosner (1960).

Abbreviations for larval measurements (Table 1) refer to Altig (1970), Anstis (1976) and McDiarmid & Altig (1989) as follows:

In lateral view: TL = total length; BL = body length; BD = max. body depth; TD = max. tail depth; TM = depth of tail musculature (in line with TD); BTD = tail depth at body terminus; BTM = depth of tail musculature at body terminus; E = eye diameter; S = diameter of spiracle at opening; SN = snout to naris; SE = snout to eye; SS = snout to spiracular opening; DF = max. depth of dorsal fin; VF = max. depth of ventral fin.

In dorsal view: BW = max. body width across abdomen; EBW = width of body at level of eyes; BTMW = max. width of tail musculature at body terminus; IO = inter-orbital span; IN = inter-narial span; EN = distance from eye to naris.

In ventral view: MW = transverse width of oral disc.

Illustrations were drawn using a drawing tube attached to the stereoscopic microscope.

DESCRIPTION OF EMBRYOS

The single female laid 556 eggs. It was not possible to make observations on the form of the egg mass, as a result of disturbance during transit. Ova were at stage 9 when first observed on 1 November, 1972. One embryo preserved at this stage had a dark brown animal pole, off-white vegetal pole and measured 2.02mm in diameter.

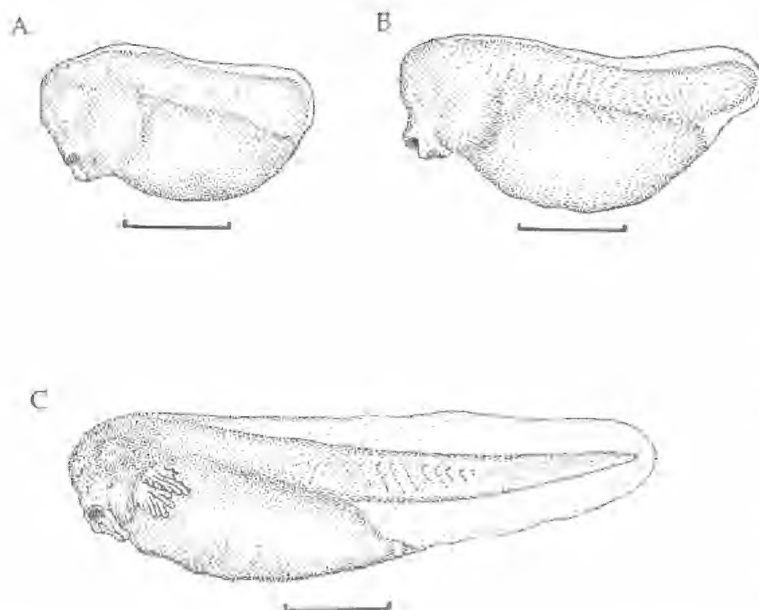


FIG. 1. Embryological stages of *L. brevipalmata*. A, early stage 17; B, stage 18; C, stage 20. Scale bars = 1mm.

By 2030 on 1 November, the embryos had reached stage 17. The tail bud is bent in this stage, making most measurements of embryo length approximate.

Embryos preserved at early stage 17 (Fig. 1A), have optic bulges, prominent gill plate bulges, a slight pronephric swelling and fine, closely aligned muscular ridges along the neural tube. There are prominent U-shaped ventral suckers joined by the stomodaeal groove. The embryos are pale brown with a pale cream yolk sac. There are a small number of melanophores around the gill plate and neural tube, and the ventral suckers are heavily pigmented.

An embryo at stage 18 has very prominent gill plate bulges (Fig. 1B). The stomodaeal groove is deeply furrowed, its rim protruding strongly forward. There is a small oral sucker at each corner. The optic bulge is quite indistinct and the tail fins are beginning to develop. The embryo is very pale cream in preservative.

The first specimen hatched at stage 20 on 2 November, 3 days after the eggs were laid. The live embryo is dark grey-brown with a light brown yolk sac. The optic region is barely discernable and the oral suckers are prominent, being still joined along the anterior edge of the stomodaeal groove, and divided medially on the posterior edge. The indis-

ting narial pits are faintly outlined with pigment. There are three pairs of external gills; 3 branches on the uppermost pair, 7 on the middle pair and 8 on the lowest (Fig. 1C). The tail musculature ridges are developing and the fins are translucent.

DESCRIPTION OF LARVAE

The only larvae available for study were one specimen at stage 37 and one at stage 41. The former specimen (Fig. 2) is described as follows:

Body ovoid in shape, widest across mid-region of abdomen. Snout broad and truncate in dorsal view and truncate in lateral view. Nares small, opening antero-laterally and outlined by a fine border of melanophores. Eyes lateral. A narrow ridge

runs from from each eye to each naris. Spiracle sinistral, ventro-lateral, not visible from above, opening postero-dorsally, with tube diameter decreasing markedly from origin to opening. Vent tube broad, median in position and opening to a diamond-shape when expanded. When relaxed, the aperture has a '<' shape, with point of '<' directing anteriorly (Fig. 2C). Opposite point of diamond-shaped opening (>) attached to edge of ventral fin.

Tail fins arched, tapering to a fine point. The dorsal fin extends onto the body up to the mid-point of the abdominal region (Fig. 2B) and in lateral view, fin is deepest just anterior to its mid-point. Ventral fin marginally deepest anterior to its mid-point. Tail musculature deepest at body terminus, then narrows, before broadening slightly near mid-point and tapering to a fine flagellum.

Oral disc antero-ventral, bordered by small marginal papillae around all but medial anterior third. A small number of submarginal papillae present. Labial teeth in two complete anterior and three complete posterior rows, each set approximately equal in length (Fig. 3). Keratinised jaw sheaths narrow, with fine serrations along the somewhat irregular inner edges.

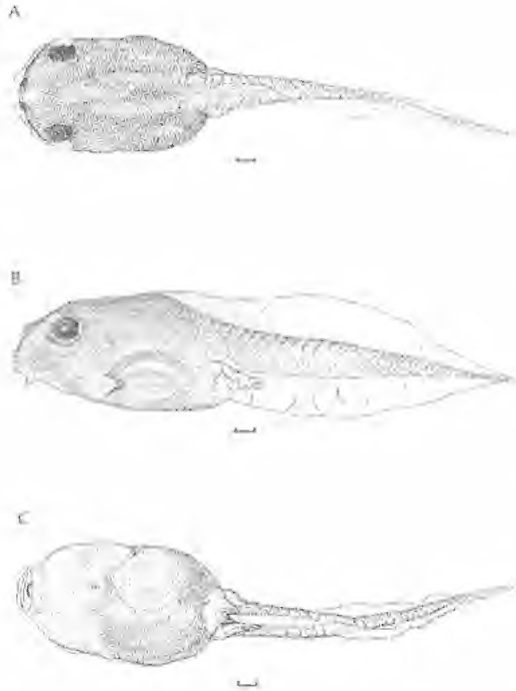


FIG. 2. Larva of *L. brevipalmata* at stage 37. A, dorsal view; B, lateral view showing cream internarial patch visible only in life; C, ventral view. Scale bars = 1 mm.

COLOUR IN LIFE

Dorso-lateral surface uniform dark brown, with a small cream patch on snout between nares (Fig. 2A). Dorsal surface of tail musculature dark anteriorly, lightening posteriorly. Ventrolateral surface with a grey blue sheen. Fins mostly transparent, with some light sandy pigment along the tail musculature in lateral view. Cream patch on snout barely distinguishable on specimen at stage 41.

COLOUR IN PRESERVATIVE

Dorsal surface of specimen at stage 37 dark brown (darkest over the intestines), but cream patch has disappeared. Tail musculature only slightly lighter than body anteriorly, becoming pale cream posteriorly. Hind limbs show some patches of melanophores.

Ventro-lateral region over intestinal mass mainly dark blue-grey, with part of intestine and fore-limb visible. Remainder of body dark brown, except for translucent region around vent. Fins and musculature have fine dusky pigment diffused over entire surface, increasing slightly towards body terminus. Musculature bordered

above and below by fine line of pigment. Specimen at stage 41 has more pigment over tail and body, and body wall is slightly less translucent.

Ventral surface dark blue/grey over intestines and anterior half translucent, with fine, diffuse pigment.

Metamorphosis was reached on 26 December 1972, 57 days after the eggs were laid. One specimen preserved immediately at stage 46 was 12.7 mm in length and shows the uniform brown of the adult over dorsum and limbs. The white labial stripe is present and there is a black canthal stripe from tip of snout to eye. A similar stripe is just beginning in the post-orbital region above the tympanum. At $\times 6$ power, numerous scattered, fine tubercles cover the dorsum. The ventral surface is white. The green pigment present in the axilla, groin and thighs of the adult, as yet has not developed.

DISCUSSION

EMBRYOLOGICAL DEVELOPMENT

L. brevipalmata is unusual in possessing 3 pairs of external gills. Only one other Australian hyloid species has been described as having 3 pairs (*L. chloris*, see Watson & Martin, 1979).

LARVAE

The tadpole of *L. brevipalmata* is the only lentic, nektonic Australian hyloid species yet described as possessing a median vent tube. Prior to about stage 41, live tadpoles may be distinguished from other sympatric ground-dwelling

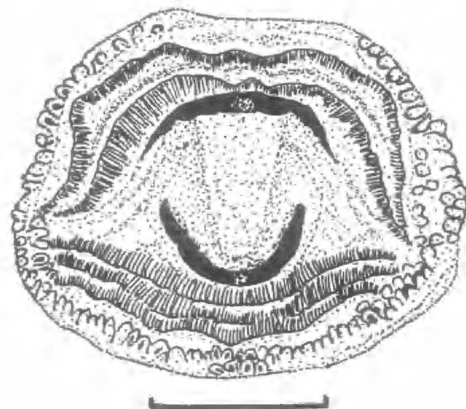


FIG. 3. Mouthparts of *L. brevipalmata* larva at stage 37. Scale bar = 1 mm.

TABLE 1. Measurements in mm. A, embryos; B, larvae; C, metamorphosis.

| A. Embryos | | |
|--|----------|-----------------|
| Stage | No. | Diameter |
| 9 | 1 | 2.02 |
| 17 | 5 | 2.7 (2.59-2.88) |
| 18 | 1 | 3.32 |
| 20 | 1 | 5.33 |
| B. Larvae (Specimens per stage = 1) | | |
| Lateral View | Stage 37 | Stage 41 |
| TL | 28.9 | 29.4 |
| BL | 11.15 | 10.66 |
| BD | 6.23 | 5.9 |
| TD | 6.72 | 6.07 |
| TM | 2.13 | 2.13 |
| BTM | 5.74 | NA |
| BTM | 2.79 | 2.62 |
| E | 1.48 | 1.48 |
| S | 0.66 | 0.57 |
| SN | 0.82 | 0.49 |
| SE | 2.29 | 1.97 |
| SS | 6.16 | 5.9 |
| DF | 2.54 | 2.79 |
| VF | 2.46 | 1.97 |
| Dorsal View | | |
| BW | 6.4 | 6.23 |
| EBW | 6.15 | 5.9 |
| BTMW | 2.62 | 1.97 |
| IO | 3.61 | 3.61 |
| IN | 1.48 | 1.31 |
| EN | 1.8 | 1.80 |
| Ventral View | | |
| MW | 2.71 | 2.30 |
| C. Metamorphosis (Specimens per stage = 1) | | |
| | Stage 46 | |
| TL | 12.7 | |

hylid species such as *L. freycineti*, *L. latopalmata* (Anstis, unpubl.), *L. nasuta* (see Tyler et al., 1983) and *L. lesueuri* (see Martin et al., 1966) by a combination of a uniform dark brown body colour, a small cream patch on the snout, median vent tube opening and two unbroken anterior rows of labial teeth.

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A PRELIMINARY ASSESSMENT OF THE SPATIAL DISTRIBUTION OF STONE ARTEFACTS FROM THE SOUTH MOLLE ISLAND ABORIGINAL QUARRY, WHITSUNDAY ISLANDS, CENTRAL QUEENSLAND COAST.

BRYCE BARKER AND RICHARD SCHON

Barker, B. & Schon, R. 1994 12 01: A preliminary assessment of the spatial distribution of stone artefacts from the South Molle Island aboriginal quarry, Whitsunday Islands, central Queensland coast. *Memoirs of the Queensland Museum* 37(1):5-12. Brisbane, ISSN 0079-8835.

Distribution of artefacts made from a black tuff raw material type in the Whitsunday region are traced by morphological similarities and petrographic analysis to an Aboriginal quarry source on South Molle Island. Although the petrographic sample size is small and relatively heterogenous there are strong indicators that the source of nearly all the volcanic tuff artefactual material found on the Whitsunday Islands and parts of the adjacent mainland are from this source. Explanations for the pattern of distribution include, proximity to raw material source, regional interaction of social networks and the extent of the Ngāro 'tribal' system. □ *Black tuff, sourcing, South Molle Aboriginal quarry, petrography, Whitsunday Is.*

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This paper presents preliminary results of a study aimed at sourcing stone artefacts, found in the Whitsunday region, to a large Aboriginal quarry on South Molle Island. South Molle Island is one of the Cumberland Islands (northern Cumberland Islands are termed the Whitsunday Islands) located on the central Queensland coast (Fig. 1). The northern Cumberland group are, according to Tindale (1974); the domain of the Ngāro, whose country extended from Hayman Island in the north down to St Bees Island in the south, including Cape Conway on the mainland coast. Surveys and excavations from islands and the adjacent mainland between Bowen and Midge Point have established an overwhelming homogeneity of artefact raw materials (Barker, 1988, 1989a, 1989b, 1990, 1991a, 1991b, 1992a, 1992b, 1992c, 1993; Hall & Barker, 1989). This material is generally characterised as a black siliceous volcanic tuff and appears identical to the raw material found on the South Molle Island quarry. It was considered that if the black tuff raw material found in the region came from a source or sources other than the quarry on South Molle, that this would be reflected in its pattern of distribution. This paper therefore, examines the distribution of stone artefact raw materials in relation to known quarry sources in the region, and presents the preliminary findings of a petrographic analysis carried out on raw material from the South Molle Island quarry, and on various artefacts from islands and coast as far distant as 100km. It is argued that the majority, if

not all, of the black tuff artefacts found on the islands, and on the adjacent mainland coast, are from this source. The rationale for this argument include: 1, the relative intensity of quarry use; 2, the fact that it is the only known culturally exploited source of black tuff material on the islands; 3, the quarry's central location to all the known sites in the region. The preliminary results from the petrography will be discussed in relation to this model below.

THE SOUTH MOLLE ISLAND QUARRY

South Molle Island is a small offshore island of 420.5 hectares, approximately 2 km from the mainland. The quarry (SMIQ) is located on the south eastern side of the island, on top of a prominent ridge just above Bauer Bay the main resort beach. Quarried raw material covers an area of 300m along a steep ridge, with flakes and other artefacts scattered down the eastern side for over 200m, and down the western side for 500m. The artefacts are up to 1m deep in places. Three circular pits, where material has been mined, line the top of the ridge (Figs 2, 3A,B). The quarry is dominated by extremely large flakes which have been removed from the substrate and then used as cores (technologically they are retouched flakes). A number of round water rolled cobble hammerstones from the beach are also present (Fig. 3C). The actual substrate from which the raw material has been struck is almost completely covered by huge densities of artefact discard (Fig. 3D). Seventy five large, backed asymmetrical

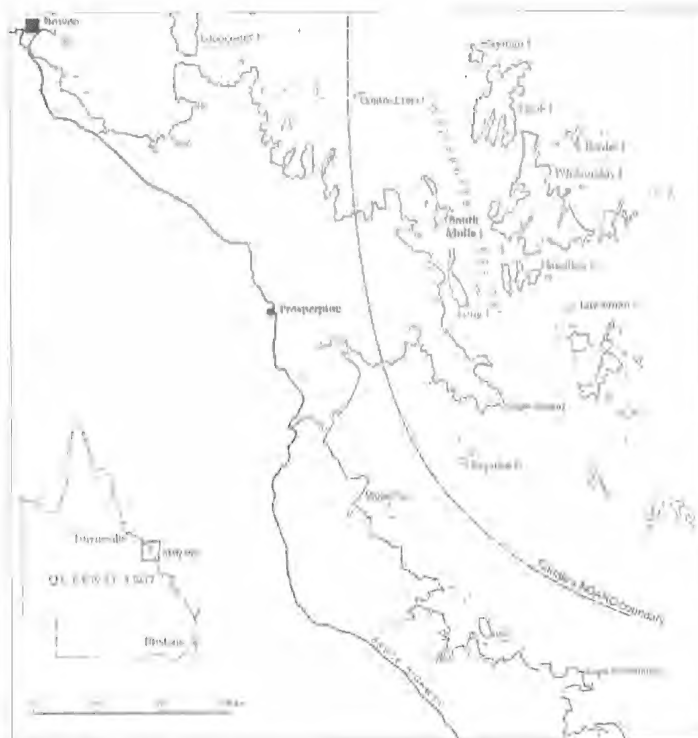


FIG. 1. The study region.

blades ('Juan Knives') were collected from the quarry site and the beach below the quarry (2 have also been found on islands) (Barker, unpubl.) in prep). The archaeological excavation of in-situ black tuff artefacts from basal strata in Nara Inlet 1 rockshelter on Hook Island, (approximately 18km east of South Molle) demonstrates the early use of the black tuff material. The near basal date of Nara Inlet 1, indicates that a minimum age for the use of the South Molle quarry can be placed at sometime prior to 8150BP (Barker, 1989a, 1991a). Analysis of excavations undertaken in 1992 of a rockshelter directly below the quarry, and on the slopes adjacent to the quarry itself, may shed further light on the quarries antiquity (Fig. 2).

Although the South Molle Island quarry would appear to represent large scale and intensive activity, this view must be tempered with the knowledge that it has probably been in use for at least 8000-9000 years. Recent estimates put the total number of artefacts on the quarry at approximately 7 million (Border, 1993) representing an artefact discard of just 2.1 per day or 766.5 per year. From 5 stratified sites excavated by Barker (1989a, 1991a, 1993) on the Whitsunday Islands, it is clear that discard of black tuff

artefacts occurred in much greater densities in the early period of occupation of the region (sometime before 8150BP until c.2,500BP). After this period, stone artefact discard rates for a 50cm x 50cm excavation square decreased from a maximum of 9.5 artefacts per 100 years in the early phase, to as little as 0.5 artefacts per 100 years during the last c.2500 years (Table 1).

The first level of analysis, in regard to the use of the quarry and the distribution of artefacts in the region, was on observed morphological similarities and differences between raw material types, and an examination of the historical record relating to use or occupation of South Molle Island. It was considered reasonable to assume that if the black tuff raw material came from South Molle Island, that the highest densities of black tuff material would be found in sites within closer proximity to this source (Renfrew, 1977; Sidrys, 1977; McBryde, 1984).

The survey work relating to this study was undertaken as a component of Environmental Impact Statements, or as part of the survey strategy designed for a research Phd project in the region (Barker, unpubl.). The Islands and the mainland coast have been extensively surveyed. The area from Southern Cape Conway down to Midgeton has also been extensively surveyed.

TABLE 1. Temporal discard of black tuff artefacts from stratified sites

| Site | Time Span | Number of Artefacts | Discard /100yrs |
|-----------------|---------------|---------------------|-----------------|
| Hill Inlet 1 | *2700-present | 49 | 1.8 |
| Border Island 1 | #2500-present | 19 | 0.7 |
| | *6400-2500bp | 352 | 9.5 |
| Nara Inlet 1H | #2500-present | 19 | 0.7 |
| | *8150-2500bp | 228 | 4.1 |
| Nara Inlet 1G | #2500-present | 15 | 0.5 |
| | *8150-2500bp | 78 | 1.4 |
| Nara Inlet AS1 | *2500-present | 37 | 1.5 |

*These dates represent basal or near basal dates

#These dates correlate with major stratigraphic change and greatly increased densities of other cultural material.

The hinterland area west of Airlie Beach and the Proserpine area have been less extensively surveyed and assemblages from these areas are described from private collections, as well as material held in the Queensland Museum, the Anthropology Museum (Department of Anthropology and Sociology, University of Queensland), the Bowen Historical Society and the Proserpine Cultural Centre.

HISTORICAL ACCOUNTS OF ABORIGINAL ACTIVITY ON SOUTH MOLLE

The most authoritative reference to the South Molle Island quarry is from Roth (1904:19) who mentions the site in the context of sources of stone for "stone celts" (edge ground axes). He notes: *'Quarries whence these celts were originally obtained are none too common, there is one on.....Molle Island in the Whitsunday Passage and at Culture Creek, or Happy Valley, about 7 miles from Proserpine'*.

Two other direct historical references to the use of the South Molle Island quarry comes from an account in a popular magazine by Henry Lamond, a former owner of the lease on South Molle Island and from W.E. Bauer, the founder of the South Molle Island resort. Both accounts are relatively recent (1930s-1950's) and may tend to be apocryphal (Lamond was a regular contributor of stories to magazines and newspapers). Lamond's source is an old Aboriginal man named Percy, who stated that the local Aboriginal population used to obtain flint for axes from South Molle Island (Lamond, 1960): *'.....they went to what we call South Molle for stone with which to make tomahawks. They called that island "Whyrriba" which meant stone axe. I should know. It was my home for exactly ten years'*.

Bauer's (1958) account is similar, stating that: *'.....the native name for South Molle was "Wer-ribee" which translated means stone flints. We have a range on the Island where this flint is very plentiful, and the natives used to make their stone axes here'*.

Although not mentioning the quarry specifically, there are other historical references relating to

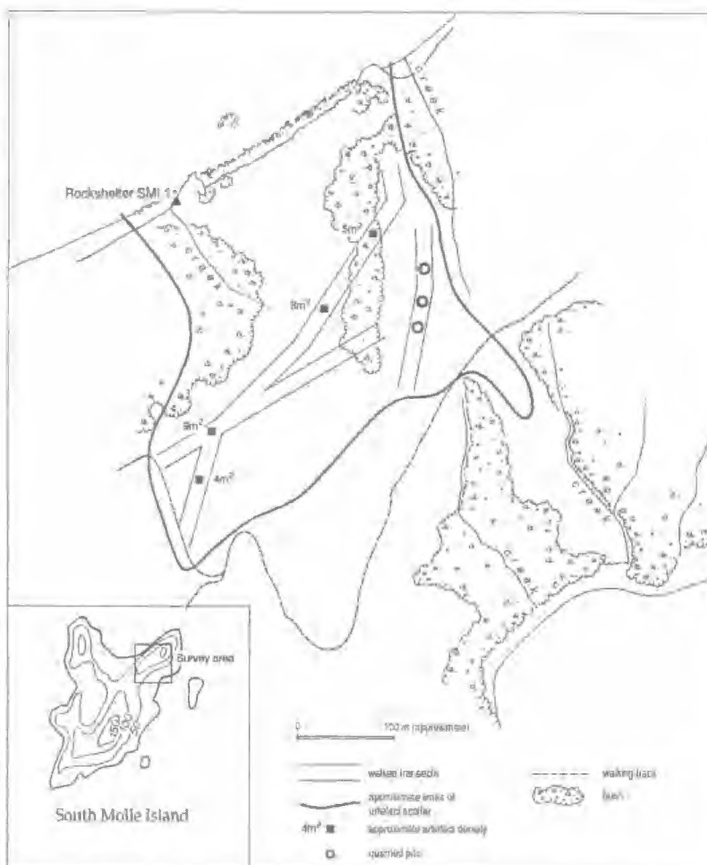


FIG. 2. South Molle Island quarry (adapted from Border, 1993).

the use of the Island itself; for example, Dalrymple (1860) on the Spitfire in 1860, stated that: *'on Lindeman and Molle Island in September dense clouds of smoke rose from the fires of the natives'*.

Dalrymple also describes an encounter with two Aboriginal men in a canoe near South Molle Island, which met them soon after leaving the Port Molle anchorage (and, therefore, probably from South Molle Island itself). Dalrymple (1860:3) states: *'.....a breeze springing up, the two aborigines left us to cross over to Hook Island, a distance of 10 miles'*.

and from an account of the wreck of the schooner 'Eva' it is stated that upon landing on Molle Island the survivors were threatened by hostile Aborigines (Loos, 1982).

Although there is clear prehistoric and historic evidence of the use of the island, the archaeological evidence does not support the idea that the quarry was used for axe manufacture. Extensive

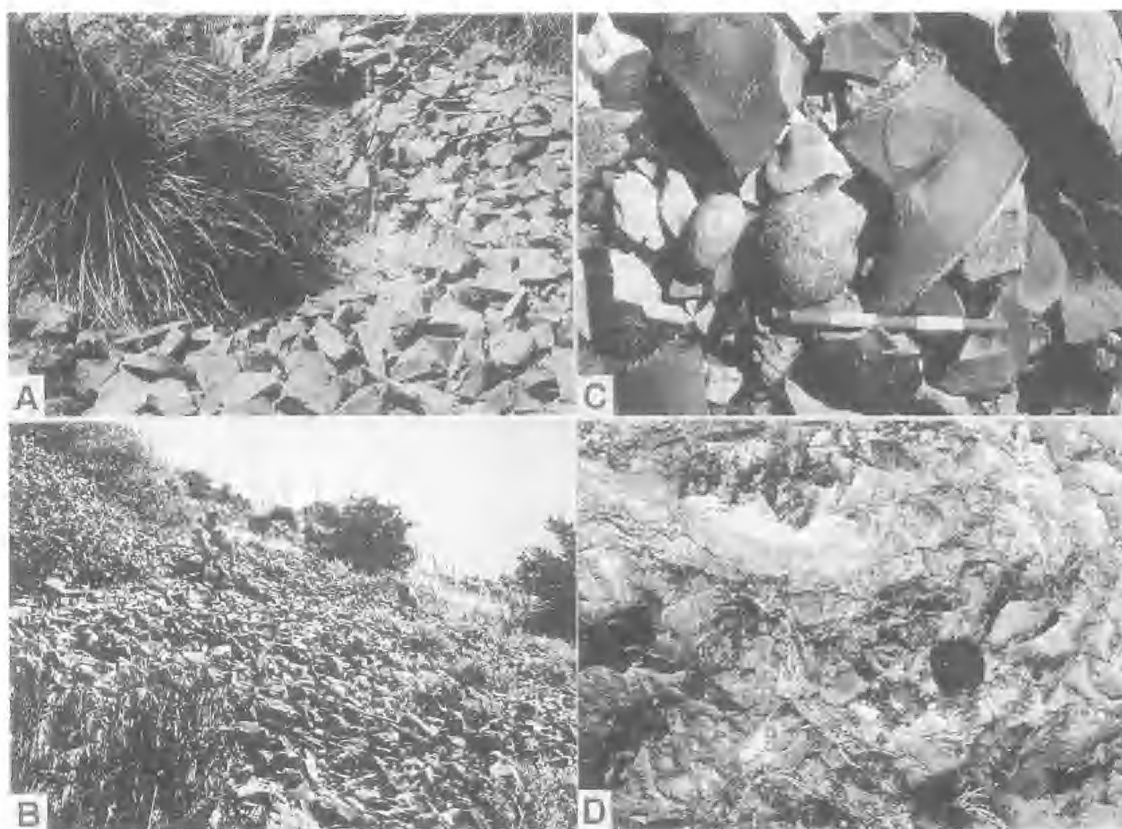


FIG. 3. South Molle Island Quarry.

surveys of axes from the mainland including private collections, collections from local historical societies, and those housed in the Queensland Museum, have not found a single axe manufactured from anything resembling the South Molle Island raw material. Generally, axes are made from rocks with a high degree of plasticity, unlike the South Molle tuff which is highly siliceous and brittle, with excellent flaking characteristics. Additionally, no axes or blanks or any artefact resembling a stage of axe manufacture has ever been found on the quarry, or in the near vicinity. It may be that Roth (1904) when stating that the quarry was used for the manufacture of stone 'celts' was referring to the large backed blades found on the quarry and the beach below it, although his description of stone 'celts' as edge ground axes seems unambiguous. Another possibility is that another source of black tuff material exists, from which axes are manufactured and it is this source which Roth (1904) mistakenly refers to as the Molle Island quarry (considered unlikely because of the acknow-

ledged accuracy of much of Roth's ethnographic accounts, and because of the lack of any evidence that stone axes were made from black tuff raw material).

OTHER RAW MATERIAL SOURCES

Although relatively extensive geological surveys have been conducted in the Whitsundays and adjacent mainland (Paine, 1972; Ewart et al., 1992; Bryan, 1991; Parianos, 1992), only one other source of the raw material resembling that of the South Molle Island material (a siliceous tuff) has been located (see below). It cannot be ruled out that other sources also occur on the islands. However, as the formation of the raw material is described as a 'pyroclastic surge deposit' which will usually occupy a relatively discreet, well defined area, it may not be easily located (Bryan, 1991). The geological conditions which create the raw material are, however, considered a relatively rare combination of factors unlikely to be duplicated often (Bryan, 1991). A number of other raw

TABLE 2. Petrographic descriptions.

| Type | Artefact | Location | Description |
|-------|----------|------------|---|
| SM | SM2 | Sth Molle | Artefacts are characterised by a fine-grained silicified tuff, black to green-grey in colour, with scattered patches of calcite alteration and quartzite/albite. The calcite alteration is characteristic of these implements |
| SM | SM4 | Sth Molle | |
| SM | W11 | Whitsunday | |
| SM | SM1 | Sth Molle | |
| SM | SM3 | Sth Molle | Artefacts are characterised by a fine and even-grained silicified tuff with sparse deformed flame and bedded opaques |
| SR | SR1 | Repulse I | |
| SR | B11 | Border I | |
| SR | H11 | Whitsunday | |
| UNCLF | MP1 | Percy I | Fine grained, strongly welded silicified ignimbrite with glass shards measuring up to 1mm |
| UNCLF | ER1 | Earl. Bay | Fine grained even-textured silicified tuff with sparse quartz veins and bedded opaques |
| UNC.F | SM5 | Sth Molle | More fine grained than the other materials with scattered opaques and traversed by quartz veins. These latter distinguish it from the SM types, to which it is otherwise similar |

material sources are known for the region. These are as follows (Fig. 5):

1, Material that superficially looks similar to the South Molle Island source was observed in a commercial quarry used by the Pioneer Shire Council. The source is located near Kuttabul (north of Mackay), 12km inland and 90km south of South Molle Island. Unlike the South Molle Island quarry, however, there is no evidence that this source was utilised during prehistoric times, although it does confirm the presence of a similar raw material type in the region.

2, A quarry source at Happy Valley on 'Culture Creek' (possibly Kelsey Creek) 11km west of Proserpine, is known from the literature (Roth, 1904) but has yet to be rediscovered or characterised. However, artefacts from around the Proserpine region are commonly made on stone that is morphologically dissimilar to that found on South Molle Island, making it unlikely that the raw material from this source is black tuff.

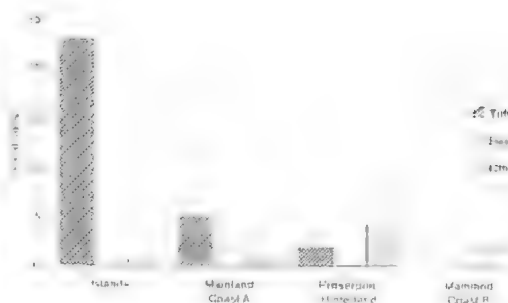


FIG. 4. Raw material sources and distribution within geographical areas.

3, Another raw material source is to be found at Blue Bay on Cape Hillsborough, where beach shingle has been quarried along an extensive area of the eastern end of the headland separating Blue Bay from Halliday Bay. This raw material is a blue-grey volcanic rock, morphologically dissimilar to the South Molle material.

4, A green volcanic material is found on South Repulse Island. Artefacts from this source have been located on South Repulse Island and Cape Conway.

In addition to these sources, the volcanic nature of the region suggests that there would be no shortage of brittle, siliceous raw material sources in the region, a raw material category ideal for stone artefact manufacture.

DISTRIBUTION OF BLACK TUFF

Most of the black tuff artefacts are found on the Islands (Fig. 5, Table 3). The mainland coast between Bowen and Southern Cape Conway (Area A Mainland coast) includes a relatively high percentage of black tuff artefacts, but also includes a range of other local raw material types. The area west of Airlie Beach, including the Proserpine region (Proserpine hinterland), has little of the material resembling the black tuff and is dominated by artefacts made from other materials. The area from Repulse Bay down to Midgeton (Area B, Mainland coast) contains no evidence of black tuff material, and is again dominated by a variety of other raw material types (Fig. 4). On this basis, it can be said that the distribution of the black tuff material, with the exception of the Proserpine hinterland, is aligned to the presence of the quarry source, with greater densities appearing nearest to the source.

TABLE 3. Number and percentage of sites with different raw materials per geographical area.

| | Tuff | | Basalt | | Other | | Total # of sites with artefacts |
|-----------------------|------|----|--------|----|-------|----|---------------------------------|
| | # | % | # | % | # | % | |
| Islands | 23 | 92 | 1 | 4 | 1 | 4 | 25 |
| Area A Mainland coast | 5 | 63 | 2 | 25 | 1 | 12 | 8 |
| Proserpine hinterland | 2 | 14 | 8 | 57 | 4 | 29 | 14 |
| Area B Mainland coast | 0 | 0 | 2 | 50 | 2 | 50 | 4 |
| | 30 | 59 | 13 | 25 | 8 | 16 | 51 |

unclassified types) are superficially similar in appearance to the South Molle raw material. We feel that once further geological analysis is completed on the South Molle Island quarry that these types will be characterised as having come from that source.

The SR1 sample is a backed implement of green tuff similar to a raw material source found on South Repulse Island and thus probably not from the South Molle Island quarry. MPI from Middle Percy Island 230km south of South Molle Island is the most dissimilar of the raw material types and is thus unlikely to be from the South Molle source.

Although the initial petrographic results are largely inconclusive, the preliminary results regarding the distribution of broader raw material types in the region, specifically the black tuff material, show that this is used almost exclusively on the islands from Hayman down to (at least) the Repulse Islands, and on the mainland coast from Bowen to Cape Conway. We feel confident that once a larger sample of the quarry has been attained, most of the artefacts found on the Whitsunday Islands (northern Cumberlands) and the adjacent mainland coast will be traced to this source. At this stage it cannot be said conclusively from the petrographic evidence that all the black siliceous tuff material found on the islands and adjacent mainland are from the one source. However, it is thought that the geographical distribution of morphologically similar material clusters around the major Aboriginal artefact quarry source on South Molle Island, suggesting that the South Molle quarry is the main, if not only source of artefactual black tuff material in the Whitsundays (northern Cumberlands) (Fig. 4).

CONCLUSION

The preliminary results of this study show that the distribution of the black tuff raw material is largely restricted to areas within the Ngaro system, either on the islands of the northern Cumberlands or the adjacent Cape Conway mainland coast. This distribution fits very closely with the boundaries for the Ngaro outlined by Tindale (1974), largely confirmed by research of one of us (B.B.) demonstrating that the quarry on South Molle Island is mainly a raw material source for

local use, despite its use over a long period of time. It could be surmised, due to the abundance of suitable raw materials throughout the wider region, that raw material of the quality of the South Molle source is common-place and, therefore, is not as likely to be used for trade or carried great distances. The highest number of sites containing this material, as well as the highest densities of this artefactual material, are those within close proximity to the known source on South Molle Island, and are found where distribution by canoe provides the easiest movement (Islands and Area A Mainland coast). It is considered that the absence of the raw material on the mainland coast south west of Cape Conway (Mainland coast B) and the coastal hinterland around Proserpine (Proserpine hinterland) and its presence at Queens Beach, Bowen over 70km to the north, may delineate the degree of interaction between the island/coastal peoples and groups directly to the south, west and north of the Whitsunday Islands.

The preliminary research carried out on the quarry and the artefacts from the archaeological sites needs further investigation. This could include technological analyses and additional geological work in order to more completely characterise the raw material from the quarry and artefacts in order to more conclusively link them to the quarry source.

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THE SPECIES OF *HAEMOPROTEUS*, *LEUCOCYTOZOOM* AND *TRYPANOSOMA* OF THE AUSTRALIAN HONEYEATER FAMILY MELIPHAGIDAE (AVES: PASSERIFORMES)

GORDON F. BENNETT, DEBORAH SQUIRES-PARSONS AND TARMO POLDMAA

Bennett, G. F., Squires-Parsons, D. & Poldmaa, T. 1994 12 01: The species of *Haemoproteus*, *Leucocytozoon* and *Trypanosoma* of the Australian honeyeater family Meliphagidae (Aves: Passeriformes). *Memoirs of the Queensland Museum* 37(1): 13-18. Brisbane. ISSN 0079-8835

The avian haematozoan species of *Haemoproteus*, *Leucocytozoon* and *Trypanosoma* occurring in the Australian Honeyeater family Meliphagidae, first described in 1909 and 1910, are re-described using modern criteria. The confusion surrounding the systematic position of these parasites when they were first described is resolved. □ *Meliphagidae*, *Haemoproteus*, *Leucocytozoon*, *Trypanosoma*, *Queensland*, *avian haematozoa*.

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Cleland & Johnston (1909) described *Haemoproteus ptilotis*, *H. philemon* and *H. meliornis* from the meliphagids *Ptilotis* (= *Meliphaga*) *chrysops*, *Philemon corniculatus* and *Meliornis* (= *Phylidonyris*) *novae-hollandiae*, which they collected by shooting at Milson Island in the Hawkesbury River and in Sydney. In 1910 they described *Trypanosoma anellobiae* from *Anellobia* (= *Anthochaera*) *chrysoptera* which was collected near Brisbane, Queensland. They obtained further samples of a number of species of meliphagids from the environs of Eidsvold, Queensland and in 1911 they identified *Trypanosoma anellobiae* from *Myzomela sanguinolenta*, *Ptilotis* (= *Meliphaga*) *fusca*, *Entomyzon cyanotis* and *Myzantha garrula* (now *Manorina melanocephala*). In 1911, they described and illustrated what they called the "intracorpuseular" or "*Leucocytozoon*" stage of *Trypanosoma anellobiae* and presented a discussion of how this stage was part of the life cycle of the trypanosome. However, the illustrations clearly indicate a species of *Leucocytozoon*. Johnston (1912) referred to *Leucocytozoon anellobiae* in a table and inadvertently established a specific designation.

Clearly, there is considerable confusion surrounding the identity of the avian haematozoa described by Cleland & Johnston from the Meliphagidae. In 1990-93, a large sample of Noisy Miners (*Manorina melanocephala*) from Laidley, Wivenhoe Dam and the Toohey Forest of Queensland were examined for blood parasites during the course of a study of their mating and social systems. These birds were infected with *Haemoproteus*, *Leucocytozoon* and *Trypanosoma*

and thus gave the opportunity to re-describe these parasites using modern criteria and evaluate their systematic position.

MATERIALS AND METHODS

Blood samples from 173 Noisy Miners (*Manorina melanocephala*) in three locations in Queensland (Laidley, Wivenhoe Dam and Toohey forest) were collected via jugular venipuncture during the period 1990-1993. A blood smear from each sample was prepared in the field, air-dried and fixed in ethanol within 12 hours. Smears were then sent to the International Reference Centre for Avian Haematozoa (IRCAH) where they were re-fixed in 100% methanol and stained with Giemsa's stain at a pH 7.2 and examined for parasites. Forty-five birds were infected with species of *Haemoproteus*, *Leucocytozoon* and *Trypanosoma* and an additional seven birds were infected with *Plasmodium vaughani*, which constitutes the first Australian record of this parasite.

The blood parasites were drawn with the aid of a camera lucida and the morphometric parameters were determined with the aid of a Zeiss MOP-3 Digital Analyser. The parameters for the haemoproteids were measured by the protocols established by Bennett & Campbell (1972) as modified by Forrester et al. (1977). The parameters used for the leucocytozoids were established by Bennett et al. (1991). The morphometric parameters and derived indices for the trypanosomes follow the generally accepted measurements for this group (Woo & Bartlett, 1982). All measurements are presented as the

mean with the standard deviation in parentheses. All photomicrographs were taken with a Zeiss Photoscope III. In the re-descriptions of the haemoproteids and leucocytozooids, the measurements for the males are not presented in the interests of brevity. However, if the dimensions are markedly different from those of the macrogametocyte, these are mentioned in text.

Through the courtesy of Dr Penny Berents of the Australian Museum in Sydney, the original material used by Cleland & Johnston was made available for study.

TAXONOMIC REVIEW

***Haemoproteus ptilotis* (Cleland & Johnston, 1909) emend. Coatney, 1936**

TYPE HOST

Ptilotis chrysops (Latham), now *Meliphaga chrysops* (Latham).

TYPE LOCALITY

Milson Island, Hawkesbury River, New South Wales.

Uninfected erythrocytes. $N = 25$. Erythrocyte $12.1 (0.8) \mu\text{m}$ in length, $6.1 (0.6) \mu\text{m}$ in width and $58.1 (7.4) \mu\text{m}^2$ in area; erythrocyte nucleus $5.2 (0.5) \mu\text{m}$ in length, $1.9 (0.2) \mu\text{m}$ in width and $7.7 (1.2) \mu\text{m}^2$ in area.

Immature gametocytes. Youngest forms seen were usually lateral to the erythrocyte nucleus, but sometimes in a polar position; margin entire.

Macrogametocyte (Fig. 1A). $N = 35$. Infected erythrocyte $12.8 (1.0) \mu\text{m}$ in length (6% hypertrophy), $7.1 (0.6) \mu\text{m}$ in width (16% hypertrophy) and $72.0 (8.6) \mu\text{m}^2$ in area (24% hypertrophy); infected erythrocyte nucleus $5.1 (0.6) \mu\text{m}$ in length (2% atrophy), $2.1 (0.3) \mu\text{m}$ in width (10% hypertrophy) and $8.5 (1.5) \mu\text{m}^2$ in area (10% hypertrophy). Parasite halteridial, entire in outline and occupying 58% of the area of the host cell-parasite complex. Parasite somewhat sausage-shaped, $12.1 (1.2) \mu\text{m}$ in length, $3.5 (0.6) \mu\text{m}$ in width at the middle of the parasite and $41.8 (6.4) \mu\text{m}^2$ in area; parasite nucleus ovoid to round in outline, median in position, $2.2 (0.1) \mu\text{m}$ in length, $1.4 (0.1) \mu\text{m}$ in width and $2.4 (0.7) \mu\text{m}^2$ in area; pigment granules average 10 (1.7) granules per parasite, small and scattered randomly throughout parasite cytoplasm; erythrocyte nucleus only slightly displaced laterally, NDR (Nuclear Displacement Ratio) = 0.6 (0.2) where the NDR represents the degree of lateral displace-

ment of the cell through the action of the parasite (Bennett et al., 1990:194), vacuoles not prominent and volutin granules not seen.

Microgametocyte (Fig. 1B). $N = 10$. Microgametocytes closely similar to macrogametocytes in all dimensions except for the larger parasite nucleus typical of the microgametocytes of all the apicomplexan parasites; parasite nucleus central with volutin granules concentrated at the poles and not occupying the area occupied by the large parasite nucleus.

BASIS OF REDESCRIPTION

Blood films 115027 and 124757 from Noisy Miners *Manorina melanoccephala* collected by Poldmaa in Queensland, Australia from Toohey Forest on 7 October 1990 and Wivenhoe Dam on 6 September 1992 respectively.

COMMENTS

Haemoproteus ptilotis is a small, halteridial haemoproteid that occupies less than 60% of the host cell-parasite complex. It has few and rather small pigment granules. It is considered to be a distinct species on the basis of its occurrence in the family *Meliphagidae*, following the assumption that haemoproteids are host family or subfamily specific (Bennett & Peirce, 1988). *Haemoproteus ptilotis* fits the description presented by Cleland & Johnston (1909) as far as can be followed. The illustrations presented by these authors are essentially the same as those figured including the few, small pigment granules per parasite. The measurements presented by Cleland & Johnston lie well within the range of those presented above. Unfortunately, the hapantotype (cotype of Cleland & Johnston, 1909) slide of *H. ptilotis* had degraded beyond use. Not only had the stain faded but the erythrocytes themselves were disintegrating and no parasites could be distinguished at any place on the blood film. In essence, the existing hapantotype slide is worthless and only the original description and illustrations of the species remains to define it.

Cleland & Johnston (1909), using the generic designation of *Halteridium*, subsequently emended by Coatney in 1936 to *Haemoproteus*, also described *Haemoproteus philemon* from *Philemon corniculatus* and their illustrations and dimensions of the parasite in this bird are essentially the same as the description for *H. ptilotis*, including the small parasite with few pigment granules. They mention that although a few of the parasites of *H. philemon* were larger than those of *H. ptilotis*, "... little difference could be detected and the identity or otherwise of the two

must await the investigation of other stages in their life histories" (Cleland & Johnston, 1909:84). They also described *Haemoproteus meliornis* from *Meliornis* (= *Phylidonyris*) *novaehollandiae*. This bird had an intense infection with many erythrocytes having multiple invasion of parasites. Their illustrations of this parasite indicate many of the parasites were immature, but the mature forms are unquestionably the same as *H. pilotis* and the dimensions of the cells are within the range of those cited in the redescription above. Regrettably, the hapantotype slide of *H. meliornis* is in equally poor shape as that of *H. pilotis* and nothing could be seen on the smear except disintegrating cells that had lost their stain and the slide is essentially worthless. The blood film of *H. philemon* was fortunate to have been cover-slipped with Canada balsam and the cells on the smear were intact although badly faded. As described originally, this smear contained cells with up to four immature parasites. However, only two mature parasites were seen and these, as far as could be determined given the lack of staining, appeared to be similar to their illustrations in 1909 and to those used in the re-description above. Although the hapantotype slides of these parasites are useless for taxonomic purposes, on the basis of the original descriptions and line drawings presented by Cleland & Johnston (1909), all three species described from the meliphagids by Cleland & Johnston are the same species. By page priority (ICZN, Section 69B (11)), therefore, *Haemoproteus pilotis* is the name of the haemoproteid in the Meliphagidae and *Haemoproteus philemon* and *Haemoproteus meliornis* fall as synonyms.

Leucocytozoon anellobiae (Cleland & Johnston, 1911) emend. Johnston, 1912

TYPE HOST

The little wattle bird, *Anthochaera chrysoptera* (Latham).

TYPE LOCALITY

Brisbane, Queensland, Australia.

Macrogametocyte (Fig. 1C). N = 51. Parasite with round morphs only. Parasite broadly ovoid to round, with a maximum diameter of 11.3 (1.6) μm , minimum diameter of 9.5 (0.9) μm , a periphery of 33.1 (3.5) μm and an area of 85.4 (15.6) μm^2 , occupying 80% of the area of the host cell-parasite complex; parasite nucleus round to

broadly ovoid and sometimes elliptical, 4.0 (0.5) μm in length, 2.8 (0.5) μm in width and 8.2 (1.9) μm^2 in area, without a marked karyosome, occupying 9.7% of the area of the parasite; vacuoles small and not prominent; volutin granules not seen; nucleus of host cell-parasite complex usually as a ribbon but sometimes as a cap, 23.1 (8.7) μm^2 in area and covering 14.9 (4.8) μm of the periphery of the parasite (44%) and occupying 21% of the area of the host cell-parasite complex; host cell-parasite complex 108.5 (22.6) μm^2 in area.

Microgametocyte (Fig. 1D). N = 14. Microgametocyte similar to the macrogametocyte in most respects except for the usual larger nucleus and pale staining that occurs in the apicomplexan parasites. The microgametocyte on average is 5-10% larger in most dimensions than the macrogametocyte and the host cell-parasite nucleus is larger and covers a greater amount of the periphery of the parasite (66% compared to 44% for the macrogametocyte).

BASIS OF DESCRIPTION

HAPANTOTYPE: Blood film no. 115021 from *Manorina melanocephala* collected by Poldmaa at Toohey Forest, Queensland on 7 October 1990.

PARAHAPANTOTYPES: Blood film no. 8872 from the Noisy Miner *Manorina melanocephala* collected by Bennett at Kenmore, Queensland on 7 September 1968, blood film no. 124710 from the same species collected by Poldmaa at Wivenhoe Dam, Queensland on 15 July 1992.

COMMENTS

This is a small round leucocytozoid, one of the smallest of the species described. It is considered to be a distinct species on the basis of the presumed familial/subfamilial specificity demonstrated for a number of species of *Leucocytozoon* (Bennett et al., 1991). Bennett & de Swardt (1989) believed that *Leucocytozoon anellobiae* also occurred in the South African Gurney's sugarbird (*Promerops gurneyi*) which was at that time classified as a meliphagid. However, this genus is now believed to have little or no relationship with the Australian Meliphagidae and has been placed in its own family, the Promeropidae (although some authorities consider them to be in the subfamily Promeropinae of the Meliphagidae). On comparison of the sugar bird material with that from the Australian noisy miner, it was evident that the South African species was much larger and that Bennett and de Swardt (1989) were in error. Therefore, the South African leucocytozoid was described as

Leucocytozoon deswardii by Bennett et al. (1992).

Cleland & Johnston (1910) described *Trypanosoma anellobiae* from *Anellobia* (= *Anthochaera*) *chrysoptera* and in 1911, elaborated on this parasite with remarks based on finding this trypanosome in several other species of the Meliphagidae. They were also convinced that the "Leucocytozoon" stage was the intracorpuseular stage of the trypanosome life cycle, a commonly held view at the time. This view may have been prompted by observation of the highly fusiform (almost trypanosome-like) appearance of *Leucocytozoon ziemanni* of owls, birds which are frequently concurrently infected with both parasites. Johnston (1912) referred in a table to *Leucocytozoon anellobiae*. The footnote to this specific name reads "The name *Leucocytozoon anellobiae* is here given to a blood parasite found by Dr. Cleland and myself in several species of birds. We believe it to be a phase in the life history of *Trypanosoma anellobiae* (Cleland & Johnston). I have used the above name as possessing specific value. Should our opinion as to the specific identity of the two forms be correct, then the name *L. anellobiae* becomes a synonym, or, to be more exact, it refers to a particular phase of *T. anellobiae*." Thus Johnston inadvertently created *Leucocytozoon anellobiae* as a valid species. Whether inadvertent or not, the name stands as the valid designation of the leucocytozoid of the Australian meliphagids and is herein so recognised. Cleland & Johnston (1910) did not indicate the disposition of the material used to define the "Leucocytozoon" stage of *Trypanosoma anellobiae*. However, when Johnston (1912) created *Leucocytozoon anellobiae*, he was in the Department of Biology of the University of Queensland. There is no trace of this material at the Queensland Museum or on record at other Australian institutions as far as is known (Lester Cannon, pers. comm.). In as much as that no "type" material was designated for *L. anellobiae*, we are designating hapantotype and parahapantotype slides from *Manorina melanocephala*, one of the hosts from which the

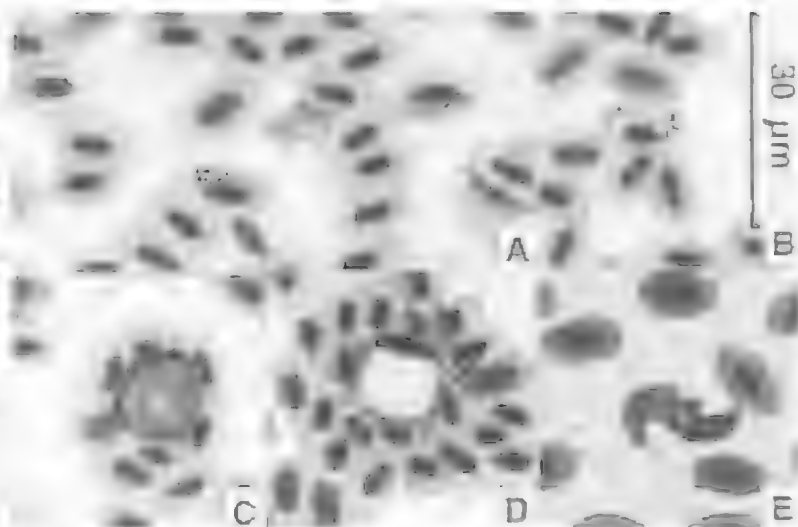


FIG. 1. A, *Haemoproteus pilotis*, two macrogametocytes; B, *Haemoproteus pilotis*, microgametocyte; C, *Leucocytozoon anellobiae*, macrogametocyte; D, *Leucocytozoon anellobiae*, microgametocyte; E, *Trypanosoma anellobiae*.

"Leucocytozoon" stage was described and are birds from the type locality.

Trypanosoma anellobiae
Cleland & Johnston, 1910.

TYPE HOST

The little wattle bird, *Anthochaera chrysoptera* (Latham).

TYPE LOCALITY

Brisbane, Queensland, Australia.

Trypomastigote (Fig. 1E). $N = 6$. Trypomastigote small and slender, averaging $25.6 (2.3) \mu\text{m}$ in length and $5.7 (0.9) \mu\text{m}$ in width at the position of the nucleus. Kinetoplast $2.7 (0.8) \mu\text{m}$ from posterior end and $9.7 (0.6) \mu\text{m}$ from the nucleus. Nucleus $12.3 (0.8) \mu\text{m}$ from the anterior end which has a long free flagellum averaging $10.8 \mu\text{m}$ (only two free flagellae measured). Trypomastigote $82.0 (12.7) \mu\text{m}^2$ in area, nucleus $15.6 (3.5) \mu\text{m}^2$ in area, the nucleus representing 19% of the area of the parasite. The distance from the posterior end to the kinetoplast represents 10% of the length of the trypanosome, while the distance of the centre of the nucleus from the posterior end is 48% of the length of the parasite, the nucleus approximately at the mid-point of the trypomastigote. The width of the trypanosome at the centre of the nucleus is 22% of the length of the organism.

BASIS OF DESCRIPTION

Blood film No. 115082 from *Manorina melanocephala* collected by Poldman at Toohey Forest, Queensland on 18 October 1990.

COMMENTS

Cleland & Johnston (1910) described *Trypanosoma anellobiae* from *Anellobia chrysoptera* (now *Anthochaera chrysoptera*) from a bird shot at Brisbane, Queensland. The infection was light and their description indicates that the trypomastigote was about 0.035 mm in length with a maximum breadth of 0.002 mm. The "kinetonucleus" was situated 0.003 mm from the posterior end. They could not see the nucleus of the organism and they did not detect a free flagellum. They concluded that the undulating membrane was very narrow and believed it to be short. Their illustrations (Plate xxxiv, figs 6, 11) are clearly those of the trypanosome illustrated in Fig. 1E of this study. The measurements they presented are closely similar to those presented herein, especially with respect to the position of the kinetoplast. It is clear that the trypanosome in the Noisy Miner is the same as that described by Cleland & Johnston. The hapantotype slide of *Trypanosoma anellobiae* was examined and found to be in the same condition as described for the hapantotype slides of *Haemoproteus ptilotis* and *H. meliornis*. Only a few of the erythrocytes were intact and the stain had faded to the extent that the blood smear was a monocolour. The blood smear was reported to also contain two species of microfilariae. However, no trace of these parasites could be found. The blood smear is unacceptable as the basis for definition of a taxon.

On the basis of the original description, *Trypanosoma anellobiae* is a small trypanosome that lacks the striated appearance and larger size of the *T. avium* group; it is also easily separated from *T. paddae*, *T. corvi* and *T. hannai* on the basis of its much smaller size and distinctive derived ratios. It is smaller than *T. bouffardi* but shares the same slender appearance of this trypanosome and also differs in that the kinetoplast is much closer to the posterior end. The length of *T. anellobiae* is within the same range as *T. everetti*, and the placement of the kinetoplast is similar in both of these species. However, *T. everetti* is a broader trypanosome (which gives the organism a "stumpy" appearance) with a nucleus that occupies about 26% of the area of the trypomastigote and cannot be confused with *T. anellobiae*. On the other hand,

T. anellobiae is remarkably similar to *T. ontarioensis* Woo and Bartlett, 1982. Both trypanosomes are small, slender and with the kinetoplast located close to the posterior end; measurements cited herein lie within the ranges quoted by Woo & Bartlett for their species. Both species have a long free flagellum that is about one-half the body length and the derived ratios are essentially the same. It would be essentially impossible to separate the two species on the basis of their morphometrics and appearance. *Trypanosoma ontarioensis* was originally described from a corvid in Ontario, Canada but its appearance is similar to the numerous small trypanosomes that have been inadequately described from South American birds and many of these South American trypanosomes can undoubtedly be assigned to this species. In addition, *T. ontarioensis* has been recorded from Sweden and appears to have a broad distribution. *Trypanosoma ontarioensis* is a readily cultured trypanosome, doing particularly well on diphasic blood-agar medium, producing infective cultured forms in two weeks. While the isolation of Australia would suggest that *T. anellobiae* is a distinct species and no attempt will be made to synonymize the two species at this time, the close similarity of the two species to each other requires experimental confirmation of their identity.

This study has also highlighted what will become a major problem for museums and repositories of hapantotype material of the Protozoa. The hapantotype material of the Cleland & Johnston species were 84-85 years of age and had deteriorated to the extent they were of no value as the basis for the definition of the taxons they were supposed to represent. It is almost 90 years since the first edition of the International Code for Zoological Nomenclature was published and the practice of establishing type material became mandatory although type material had frequently been designated decades before. Stained protozoal and similar material does age with time and as indicated in this study, in 85 years had deteriorated beyond use. While the use of coverslips and mounting media does aid in the preservation of the cells, the problem of stain fading over a long period still occurs. The preservation of hapantotype material will become a serious problem that will have to be addressed by curators of this type of material and should be addressed as a priority by the International Commission for Zoological Nomenclature.

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A REVIEW OF *Heteropodrilus* FROM SOUTH-EAST QUEENSLAND (ANNELIDA: OLIGOCHAETA)

ROB J. BLAKEMORE

Blakemore, R.J. 1994 12 01: A review of *Heteropodrilus* from south-east Queensland (Annelida: Oligochaeta). *Memoirs of the Queensland Museum* 37(1):19-39. Brisbane. ISSN 0079-8835.

The endemic earthworm *Heteropodrilus* Jamieson, 1970, is revised to accommodate four new species, plus new combinations mainly from *Plutellus* s. lat., that raise the generic total from ten to nineteen species. Previous emendments to these two genera, both of which display nephropore alternation, had reduced primary differentiation to absence or presence of stalks on the calciferous glands. In the current revision, however, the form of prostatic glands is considered more definitive. Possession of tubular prostates qualifies *Plutellus*, now restricted to three known species, while in *Heteropodrilus* there is development from this plesiomorphic state to the more derived racemose or tubuloracemose form of prostate. *Heteropodrilus* has an extensive distribution in the eastern subregion of Australia yet it appears especially diverse in south-east Queensland, compared to *Plutellus* s. strict. that is mainly restricted to central coastal New South Wales. Redescription of the type species of both genera, *H. tryoni* and *P. heteroporus*, confirms the basis of this revision. The distributions and ecology of these and other described species are considered and new keys to genera are provided. □ *Heteropodrilus*, *Plutellus*, calciferous glands, taxonomy, earthworm ecology.

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The current study resulted from part of a project investigating the distribution and ecology of earthworms in managed soils and their effects on soil fertility in south-east Queensland. Surveys located 44 exotic species that were often abundant and widely distributed, as well as 41 native taxa that were generally more restricted in their distributions. This paper concerns the indigenous *Heteropodrilus* Jamieson, 1970 that has not been extensively revised since its designation. This genus is frequently encountered in the wider Brisbane region.

Fletcher (1889) was the first to recognise a well-marked group of species (which he nevertheless referred to *Cryptodrilus*, Fletcher, 1886) sharing, amongst other characters, nephropore alternation. It was left to Jamieson (1970) to formally define *Heteropodrilus* for ten (plus one dubious) 'heteropore' species, many of which were by then assignable to *Woodwardiella* Stephenson, 1925. In the same paper, a restriction of the heterogeneous assemblage attributed to *Plutellus* Perrier, 1873 was suggested (as envisaged by Gates, 1961), as only *P. manifestus* (Fletcher, 1889) from central New South Wales appeared to be congeneric with *P. heteroporus*, the type-species. Re-description of type material confirmed the basis for a restriction of *Plutellus*

to species with tubular prostates, but this was deferred (Jamieson, 1971a,b). A numerical analysis by Wallace (1972) confirmed these groupings even though prostate morphology was withheld as an attribute.

In order to accommodate two new heteropore species from Queensland that bore racemose prostates it was necessary for Jamieson & Nash (1976) to emend the generic definition of *Plutellus* to include both tubular and racemose prostates thus reducing the distinction from *Heteropodrilus*. Such 'infrageneric variation' was used by these latter authors to 'strongly refute' the use of racemose prostates to distinguish a family Megascolecidae from a family Acanthodrilidae with tubular prostates (and holonephridia) as advocated by Gates (1959) and rejected by Jamieson (1971). However, a primitive 'plutelloid' from Lord Howe Island (Jamieson, 1977) seemed to have more in common with its congeners in New South Wales. The definition of *Plutellus* was further modified by Dyne (1981) to receive three new species from the periphery of the Morton Bay Region, bringing the generic total to eight, and the 'tenuous' distinction from *Heteropodrilus* was reduced principally to the presence or absence of stalks to the calciferous glands.

The wide distribution of *Heteropordrilus* from Queensland to Victoria corresponds in part with various riverine systems (Jamieson, 1970). It appears especially aggregated, or rather the reports are more frequent, in the Brisbane region of south-east Queensland. In contrast, *Plutellus* s. lat., was recorded further south in coastal New South Wales and just to the south and north of Brisbane. Dyne (1981, 1984) found this distribution pattern enigmatic because no appreciable biogeographic barriers intervened. He also intimated that should intermediate forms with short-stalked calciferous glands be found, it would be doubtful that the two genera could remain discrete.

The present study contends that just such intermediate forms already existed in *Plutellus* s. lat., moreover 'short-stalked' calciferous glands had also been confirmed in *Heteropordrilus*, but the consequences are here interpreted in a different manner. The apparent discontinuity of the distributions is largely resolved by revision of the definitions of both genera, based on new material and re-examination of previous accounts, resulting in an amalgamation of the 'northern' heteropores while maintaining the 'central' plutelloids as a discrete zoogeographic and phyletic entity.

CONVENTIONS

Original illustrations, drawn using a Wild M5 microscope with camera lucida, have shaded clitella. All scale bars represent 1mm.

Abbreviations used are: i ii etc., segments numbered from the peristomium; ii/ iii/ etc., on ii, on iii etc.; 1/2 2/3 etc, intersegmental furrows, i.e., between i and ii etc.; *a b* etc., individual setae from the ventralmost on each side; A B etc.; longitudinal series between setae *a* setae *b* etc.; g.m. genital marking; n.p. nephropore; NSW, New South Wales; Qld., Queensland, QMG, Queensland Museum registration number; sp.p., spermathecal pore; ; U. (convention from German) circumference. Setal ratios, of debatable systematic importance, follow the formula (xii/aa:ab:cd:dd:u).

SYSTEMATICS

Heteropordrilus is emended to accommodate, the new species, and to receive several species that were previously placed in *Plutellus* (sensu Jamieson & Nash, 1976; Dyne, 1981). The revision proceeds in three stages. First, at least two species (*H. jamiesoni* sp. nov. and *H. ox-*

leyensis) belonging to the established *Heteropordrilus*, are found to have short-stalked calciferous glands thereby expanding the generic definition to species with sessile or short-stalked calciferous glands. Hence the distinction from *Heteropordrilus* of the only '*Plutellus*' species reported from Queensland, *P. incommodus*, *P. raveni* and *P. notatus*, which are all described with similar short-stalks, is removed. Secondly, expanding the definition to include Dyne's (1981) 'intermediate' species with short-stalked glands and racemose or tubuloracemose prostates absorbs the two species from northern New South Wales, *P. minyoni* and *P. clarkei*. Thirdly, *Plutellus* is restricted to only those species with tubular prostates and long-stalked calciferous glands.

This division is especially strong as no genetic correlation between prostate form and calciferous nexus is implied. Tubular prostates are generally considered the plesiomorphic condition, thus *Heteropordrilus* can be viewed as a derived, apomorphic sibling group of a more primitive *Plutellus*. The above split has the added convenience of making the geographic distributions disjunct with *Plutellus* confined to the coastal region of central New South Wales (two species) and Lord Howe Island (one species) and the remainder in *Heteropordrilus*, chiefly in south-east Queensland and northern New South Wales. The question of the phyletic relationships of the Lord Howe Island plutelloids, is not ventured here.

Heteropordrilus Jamieson, 1970 emend.

TYPE SPECIES

Heteropordrilus tryoni (Fletcher, 1890) from Milton, Brisbane.

DIAGNOSIS

Moderate to large size terrestrial worms (52-580mm long) generally with less than 200 segments (range 90-387). Sometimes dorsum canaliculate and with or without brown-grey pigmentation. Prostomium variable from propilobous to tanylobous, often grooved. Setae 8 per segment (only occasionally *a* and/or *b* retained on xviii). Dorsal pore from 5/6 or beyond, Male pores and pores of one pair of racemose to tubuloracemose prostates in xviii. Spermathecal pores 2-5 pairs, the last in 8/9 (*H. notatus* and *H. clarkei* near mid-ix). Nephropores conspicuous at the anterior border of their segments in D lines in ii-iv or v; in C lines, or

alternating between D and C (or mid-BC) for a few segments; then from x where alternation between B and D lines commences for the remainder of the body (may be asymmetrical).

Gizzard in v. Calciferous glands, 3-5 ventrolateral pairs sessile or on short-stalks (i.e. about as long as broad) on the oesophagus, the last pair always in xiii. Spermathecae have one or more, discrete or composite, diverticula. Holonephric with (adiverticulate but sometimes bilobed) terminal bladders. Holandric, testis and funnels free or in unpaired (pericardiac) testis sacs.

DISTRIBUTION

Murray-Darling River basins in NSW and South Australia; the Wimmera River, Victoria; Tweed River basin in northern NSW; river catchments in south-east Qld.

SPECIES OF *HETEROPORODRILUS*

The numbers and conditions of specimens inspected in previous definitions (in brackets) indicates the stability of those descriptions. Only species with an asterisk are (re)described in this paper.

1. **H. bongeen* sp. nov. from Bongeen, Qld.
2. *H. canaliculatus* (Fletcher, 1889) from Lachlan River, Forbes, NSW.
Cryptodrilus canaliculatus Fletcher, 1889: 1534-1536 (twelve specimens, poorly preserved); Fletcher, 1890: 996.
Plutellus canaliculatus; Michaelsen, 1900.
Heteroporodrilus canaliculatus; Jamieson, 1970: 111-112 (types no longer traceable).
3. *H. clarkei* (Dyne, 1981) comb. nov. from Whian Whian State Forest, northern NSW.
Plutellus clarkei Dyne, 1981: 97, figs 1a; 2c, e; table 1 (three specimens)
4. *H. cooraniensis* (Spencer, 1900) from Cooran, Qld.
Cryptodrilus cooraniensis Spencer, 1900: 42-43, figs 34, 35, 36 (spirit specimens); Sweet, 1900: 114; Jenz & Smith, 1969: 86 (only one questionable syntype remains in reasonable condition).
Woodwardia cooraniensis; Michaelsen, 1907: 162; Bage, 1910: 234-236, figs 18-21.
Heteroporodrilus cooraniensis; Jamieson, 1970: 112-113 (material not available).
5. **H. dioecius* (Stephenson, 1933) from Toowoomba, Petrie, Brookfield and Samford (new record), all in Qld.
Woodwardiella dioecia Stephenson, 1933: 910-912, figs 9; 10 (four clitellate specimens).

Heteroporodrilus dioecius; Jamieson, 1970: 113-114, figs 5d-f; 9b; 10b, c (four clitellate and one acitellate specimens).

6. **H. doubei* sp. nov. from Lismore, NSW.
7. *H. incommodus* (Jamieson & Nash, 1976) comb. nov. from Eudlo Creek and Forest Glen, Qld.
Plutellus incommodus Jamieson & Nash, 1976: 47-49, figs 1: a, b; 2a-g; table 1 (14 specimens).
8. **H. jamiesoni* sp. nov. from Mt Glorious, Qld.
Heteroporodrilus ashworthi (Stephenson, 1933) syn. nov. (part, Mt Glorious specimen non Stephenson, 1933 specimen) sensu Jamieson, 1970: 109-111, figs 2; 3a; 8a,b; 9a; 10a (one clitellate specimen).
Note: *H. ashworthi* sensu Jamieson (1970) is not the same as *W. ashworthi* Stephenson, 1933, but represents a new species. Since *W. ashworthi* is a junior synonym of *H. oxleyensis* (Fletcher, 1889) the name *ashworthi* is unavailable and *H. ashworthi* sensu Jamieson (1970) is described herein as *H. jamiesoni* sp. nov.
9. *H. lamingtonensis* (Jamieson, 1970) comb. nov. from O'Reilly's, Lamington Nat. Park, Qld.
Plutellus lamingtonensis Jamieson, 1970: 115-117, figs 5a; 9c; 10d (a single specimen).
10. *H. mediterreus* (Fletcher, 1887b) from banks of the Darling River between Bourke and Brewarrina NSW; Gragin and Warialda, NSW.
Cryptodrilus mediterreus Fletcher, 1887b: 614-616 (ten specimens - lost).
Heteroporodrilus mediterreus Jamieson, 1970: 117-120, figs 4a,b,e,f,g; 9d; 10e (six poor specimens, only two clitellate).
Note: The records by Jamieson (1970: 119) for this species in Victoria are incorrect.
11. *H. minyoni* (Dyne, 1981) comb. nov. from Whian Whian State Forest, northern NSW.
Plutellus minyoni Dyne, 1981: 100-102, figs 1b; 2a, b, d; table 1 (a single intact specimen and several anterior amputees).
12. *H. notatus* (Dyne, 1981) comb. nov. from Cooroy, Qld.
Plutellus notatus Dyne, 1981: 102-104, fig 3 a-c; table 1 (three specimens).
13. **H. oxleyensis* (Fletcher, 1889) from Oxley; Brookfield (new record), Samford (new record) and Mt Cotton (new record), all near Brisbane, Qld.; ?Marrickville, NSW.
Cryptodrilus Oxleyensis Fletcher, 1889: 1537-1538. (one complete but acitellate specimen and two other "more or less incomplete specimens").

- Plutellus fletcheri* (part); Michaelsen, 1900: 173 (excluding *Cryptodrilus fletcheri* Beddard, 1887).
Woodwardia oxleyensis; Michaelsen, 1907: 162.
Heteroporodrilus oxleyensis Jamieson, 1970: 120-122, figs 3b-e; 5g; 9e; 10f,g (two clitellate specimens).
Woodwardiella ashworthi Stephenson, 1933: 912-914, figs 11-13, syn. nov. (a single clitellate specimen).
Heteroporodrilus ashworthi; Jamieson, 1970: 109-111 (part excluding Mt Glorious specimen).
14. *H. raveni* (Jamieson and Nash, 1976) comb. nov. from Forest Glen, Qld.
Plutellus raveni Jamieson & Nash, 1976: 50-52, figs 2h-j; 3, table 1 (six specimens).
15. *H. shephardi shephardi* (Spencer, 1900) from Horsham, (and Dimboola?) Victoria (Wimmera River).
Cryptodrilus shephardi Spencer, 1900: 40-41, figs 28, 29, 30, ("spirit specimens"); Jenz & Smith, 1969: 91 (three lectotypes remain).
Woodwardia shephardi; Michaelsen, 1907: 162.
Heteroporodrilus shephardi shephardi Jamieson, 1970: 122-124, figs 4c,d; 9f; 10i (a paratype specimen).
16. *H. shephardi armatus* Jamieson, 1974 from Penola and Naracoorte, Victoria (about half a dozen specimens).
Heteroporodrilus shephardi armatus Jamieson, 1974: 85-87, figs 2h; 10b; 11a; 13, table 3 (four or five specimens).
17. *H. sloanei* (Fletcher, 1889) from Connabarabran, NSW.
Cryptodrilus Sloanei Fletcher, 1889: 1536-1537, (four acitellate specimens and one doubtful juvenile).
Plutellus sloanei; Michaelsen, 1900.
Heteroporodrilus sloanei; Jamieson, 1970: 124, (three desiccated specimens).
 Note: Jamieson (1970) considered synonymy with *H. canaliculatus* and *H. lamingtonensis* dependent on availability of new material.
18. **H. thompsoni* sp. nov. from Brookfield, Qld.
19. **H. tryoni* (Fletcher, 1890) from Milton, Sherwood, Brookfield and Toowong suburbs of Brisbane; Binna Burra, Lamington National Park; Mt Glorious; Mt Mee and Nambour, all in Qld.
Cryptodrilus Tryoni Fletcher, 1890: 994-996, (one poorly preserved specimen).
Plutellus tryoni; Michaelsen, 1900: 171.
Woodwardia (?) *tryoni*; Michaelsen, 1916: 62.
Woodwardiella tryoni; Boardman, 1932: 127-128 (a single, poorly preserved specimen).
- Heteroporodrilus tryoni*; Jamieson, 1970: 125-129, figs 5b,c; 8c,d; 9g,h; 10j (nine clitellate specimens).
Woodwardiella youngi Boardman, 1932: 128-130, fig 2 (two specimens).

SPECIES INCERTAE SEDIS

?*Heteroporodrilus fletcheri* (Beddard, 1887), provenance in Qld. unknown.

Cryptodrilus fletcheri Beddard, 1887: 544-548, illustr. (two specimens, one mature - types lost).

Plutellus fletcheri; (part excluding *H. oxleyensis*) Michaelsen, 1900: 79.

Heteroporodrilus ? *fletcheri*; Jamieson, 1970: 114-115.

Note: Based on inadequacies of the original account, Jamieson (1970) considered this species to be 'nomen et species dubium' but its affinity with *H. oxleyensis* was alluded to by Michaelsen, 1900.

A large heteropore specimen, unfortunately too macerated for adequate characterisation, was collected by C.H. Thompson in 1984 from Mt Buderim near Maroochydore, Qld. It had the external appearance of *H. shephardi* and three pairs of spermathecae. Two unpublished new species from south-east Qld. have been identified by Dyne (1984) and a further two species from the Adelaide region are currently in preparation by the author.

KEY TO HETEROPORODRILUS

1. Large size (250mm); five pairs of calciferous glands; three pairs of spermathecae . . . *H. tryoni*
 Four pairs of calciferous glands 2
 Three pairs of calciferous glands 10
2. Three pairs of spermathecae 3
 Two pairs of spermathecae 8
3. Nephropores alternate between *c* line and *d* line in 4/5-8/9 (from Queensland) 4
 Nephropores alternate between *d* line and mid-*bc* in 4/5-8/9 (Victoria and South Australia) . . . 7
4. Prostates confined to xviii, penial setae absent; genital markings usually in xx 5
 Prostates xvii-xix or xvi-xxii, penial setae present; no genital markings in xx 6
5. Prostates with straight duct; spermathecal diverticula variable, single or paired *H. incommodus*
 Prostates ducts long and sinuous; spermathecae each with a single, simple diverticulum . . . *H. raveni*
6. Dorsum canaliculate; spermathecae each with two diverticula, occasionally single, but often compound; seminal vesicles in ix and xii *H. canaliculatus*
 Body circular; spermathecae each with a single, simple (even rudimentary) diverticulum; seminal vesicles in xi and xii *H. mediterraneus*

7. Genital markings as eye-like pits in 17/18 and 18/19; penial setae present in xviii

..... *H. shephardi armatus*

- Genital markings segmental in some or all of xvii, xviii and xix; penial setae absent

..... *H. shephardi shephardi*

8. Spermathecal diverticula bifid or trifid or variously multi-lobed or numerous, genital markings in x (or xi) 9

- Spermathecae with simple (paired) diverticula

..... *H. bongeen* sp. nov.

9. Size 210mm; prostomium epilobous furrowed; spermathecae with large and concertinaed ampullae and compound diverticula

..... *H. thompsoni* sp. nov.

- Size <105mm; prostomium tanylobous; spermathecae, with simple or bifid diverticula, opening to midsegment *H. notatus*

10. Spermathecae, three or more pairs 11

- Spermathecae, two pairs 14

11. Size generally 100mm; genital markings in xvii-xx 12

- Size generally <100mm; genital markings weak or absent (immature?) 13

12. Spermathecae 5 (or 4) pairs; genital markings widely paired in xvii-xx, presetal in xvii

..... *H. jamiesoni* sp. nov.

- Spermathecae 4 (or 3) pairs; postsetal genital markings elongate or closely paired in xvii-xx

..... *H. oxleyensis*

13. Spermathecae 3 pairs each with two diverticula

..... *H. sloanei*

- Spermathecae 3 pairs (occasionally one of the six absent) each with a single diverticulum; prostates absent or present *H. dioecius*

14. Spermathecal pores segmental, presetal in viii and ix *H. clarkiei*

- Spermathecal pores intersegmental in 7/8 and 8/9 15

15. Size 300; prostomium epilobous; preclitellar genital marking a series of papillae within tumid ventral pads in xii, xvii-xxi *H. minyoni*

- Size 100; prostomium epilobous; preclitellar genital markings in vii, viii and ix; spermathecal diverticula paired *H. doubei* sp. nov.

- Size <80; prostomium tanylobous; preclitellar genital markings widely paired or lacking 16

16. Spermathecal diverticula paired

..... *H. lamingtonensis*

- Spermathecal diverticula single

..... *H. cooraniensis*

Associations between species can be inferred from their nearness in the above key. Accounts of species not covered in the following descriptions may be sought with reference to the preceding species list.

DESCRIPTIONS OF SPECIES

Heteroporodrilus bongeen sp. nov. (Fig. 1)

MATERIAL EXAMINED

HOLOTYPE: QMG210136, opposite the local school house at Bongeen (27°34'S; 151°27'E) on the Condamine River plain west of Toowoomba, Qld, R.J. Blakemore, 09 Apr 92, drawn and dissected, posterior amputee.

PARATYPE: same collection data as holotype. QMG210137, dissected, posterior amputee.

OTHER MATERIAL: same collection data as holotype. QMG210138, two anterior amputees (losing first 5-7 segments); also collected were four damaged sub adults.

HABITAT

Under bare soil in dark brown cracking clays, Waco clay gilgai complex (Beckmann & Thompson, 1960) on roadside next to cultivated fields.

EXTERNAL CHARACTERS

Length 250+mm, body circular in section without dorsal groove although one specimen had the posterior 6 segments furrowed. Width 5.5-7.5mm, widest point about viii.

Mass 3-4g per adult. Segments 193-200, first ten segments smooth followed by moderate secondary annulation in succeeding segments. Colour dark slate grey pigmented anterior (with paler ventral tumescences on x, xi and possibly xii), dorsum and caudal segments with faint red/yellow iridescence; mid-body moderate pigmentation (soil visible in gut). Clitellum variously darker or lighter brown colour. Prostomium open epilobous or closed by fine groove but appearing tanylobous due to longitudinal dorsal groove extensions which may almost reach as far as 1/2. First dorsal pore 10/11? (difficult to determine due to deep furrows). Setae small, 8 per segment from ii, *a* and *b* obscure (modified?) on xviii, lateral setal couples *cd* widely spaced (mean of two ratios, 1.7:1.0:1.4:2.4:0.28). Nephropores in D line 1/2-3/4, 6/7, 8/9, 10/11 or 11/12 then alternating; in B line 5/6, 11/12 or 12/13 then alternating, possibly in C line in 4/5-7/8. There is slight variation between specimens, but for most of the body length there is clear alternation between B and D lines. Clitellum 1/3xiii-xvii annular, setae and nephropores retained. Male pores minute in xviii on small raised porophores in B line. Female pores paired in xiv in line of anterior annulus within a common

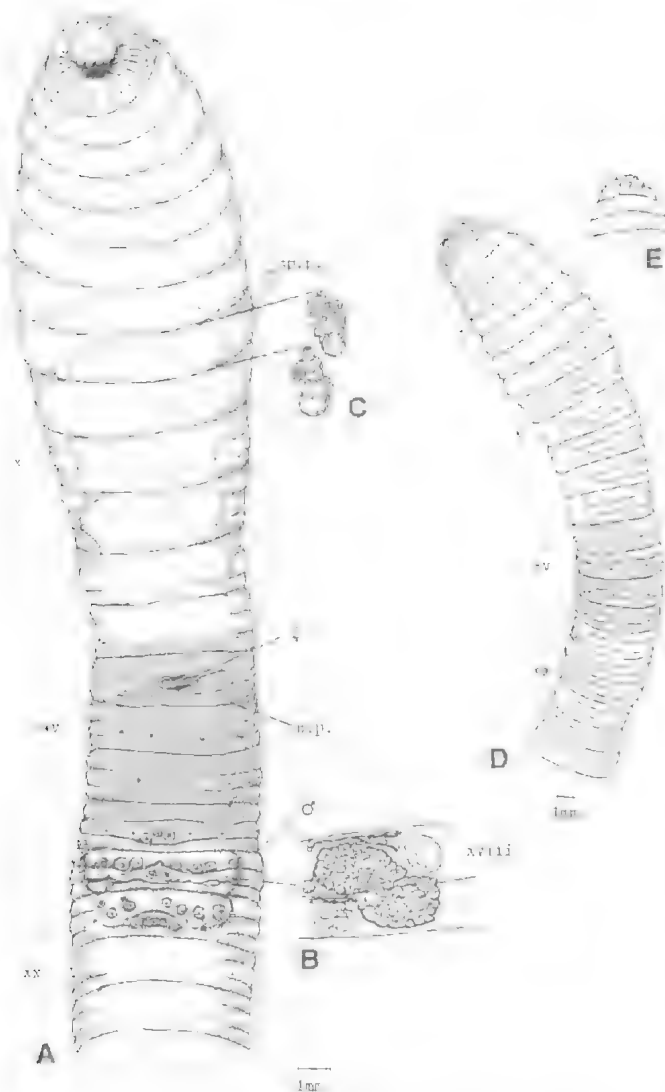


FIG. 1. *Heteroporodrilus borgeen* sp. nov. A, ventral view of H specimen; B, prostate (with two adjacent nephridia); C, spermathecae in situ; D, reduced lateral view; E, prostomium.

darker patch antero-medial to *a* setae. Spermathecal pores 7/8 and 8/9 in B line concealed in deep intersegmental furrows. Genital markings (x-xii ventrally tumid?), in xvii almost central between *a* setae, three small discs in raised tumid area; in xviii, especially in anterior annulus, four or five pairs of discs (one pair ventral in setal arc) in furrowed, generally tumid area that fills the ventral aspect; in xix similar markings, but discs tend to be smaller and more numerous.

INTERNAL CHARACTERS

Septa 4/5-11/12 getting progressively thicker, from 12/13 becoming weaker (10/11-12/13 thickest); pharyngeal ligatures (tendons) extend beyond viii. Dorsal blood vessel single, continues on pharynx. Commissurals in vi-ix, larger hearts in x-xiii. Gizzard compact, spherical and muscular in v. Calciferous glands four pairs, compact and ventral on oesophagus in x, xi, xii, and xiii; those in x smaller, almost rudimentary. Oesophagus narrows in xiv (valve?) then widens in xv as intestine proper; typhlosole not found. Holonephridia, a pair in each segment, from at least v, with large deflated and flattened, spherical terminal bladders. Nephridia closely associated with anterior septa (pre-septal funnels). Male organs holandric: iridescent funnels of testes in x and xi; racemose seminal vesicles in ix and xii. Ovaries in xiii, ventrally paired sheets of mesentery may be ovaries but individual oocytes not seen, the egg funnels were seen on the posterior septum. Five or six smallish, white spheres were noted in one specimen loosely attached to the septum, possibly parasitic *Monocystis* sp? Prostates a pair of large tongue-like racemose glands extending from xviii-xix and overlying a small, flaccid duct that soon enters the body wall. Spermathecae two pairs in viii and ix: waisted ampullae clearly demarcated from shorter ducts, each bearing a pair of opposed digitiform, iridescent diverticula.

One specimen had a single diverticulum on only one of its spermathecae. Gut contents fine grey clay soil and a few round grits coated in mucus (i.e. geophagous).

TAXONOMIC REMARKS

H. borgeen has 4 pairs of calciferous glands and 2 pairs of (bidiverticulate) spermathecae. It is perhaps closest to *H. canaliculatus* (Fletcher, 1889) recorded from the Lachlan River at Forbes, NSW. It differs from *H. canaliculatus* in several

features but especially in lacking dorsal canaliculation, in having one fewer pairs of spermathecae and in the numbers and position of the genital markings. On these variations, together with its geographic location, it is separated from other species and it is named after its type location.

ECOLOGICAL/AGRONOMIC OBSERVATIONS

In the same samples, a native *Diporochaeta* sp. was also identified. Neither of these, nor any other worms, were found nearby, including under an adjacent sorghum (*Sorghum bicolor*) crop, despite an hour of searching. Perhaps cultivation, which has severe effects on burrow systems and soil physical properties, and aerial spraying of insecticides, are adverse to its survival. The worms were collected from opposite the local school and thereby in an area presumably less affected by application of biocides. A local farmer from Jondaryan (K. McIntyre, pers. comm.) reported that when the natural grasslands were first cultivated, masses of earthworms were exposed. Possibly the present population is residual from what must have been a very abundant fauna. The type locality was known to local fishermen in the 1950's as a good source of bait (C.H. Thompson, pers. comm.).

The behaviour of these long worms was to escape rapidly along their burrows but when caught they were only moderately active, although they exuded copious watery fluid which dripped from their bodies. The specimens were dug from burrows up to 1cm wide to a depth greater than 30cm. Waco clay is a strongly structured soil that has a thin, fine granular 'self-mulching' surface, but it is possible that the surface casting noted for this worm contributed to the granular aggregates observed. It is likely that their burrows extend down to the deep calcareous brown clay subsoils found at depths of up to 1m as during dry periods these deep subsoils would provide a moist retreat for earthworms.

The agronomic potential of collected specimens was investigated in a glasshouse experiment, probably the first assessment of this type for this genus. From twelve specimens, maintained in a sealed container filled with the soil for six months, four mature specimens (which had regressed to a "sub-adult" stage with suppressed clitella) were released into new soil in irrigated 18kg cores of clay. None survived after four months (October 1992-February 1993) when soil temperature ranged 17-35°C. Despite this, their burrows and granular casts indicated some

initial activity and the final yield of grain sorghum (*Sorghum bicolor*) was increased, compared to uninoculated controls, by 40%.

Heteropodrilus dioecius (Stephenson, 1933) (Fig. 2)

MATERIAL EXAMINED

2 mature specimens, QMG216139, Brookfield, Qld (27°30'S, 152°55'E), C.H. Thompson, 17 May 92; CSIRO Samford farm, Qld. (27°22'S, 152°53'E), 5 mature specimens, R.J. Blakemore, 9 Apr 92 and 22 Jun 92, in author's collection.

HABITAT

Under litter on bank of river; on surface after rains.

EXTERNAL CHARACTERS

Length 58-70mm. Width 2.5-3mm. Segments 90-103, body cylindrical but segments tending to become trapezoid with only slight secondary annulation. Colour of anterior dorsum pigment light to dark brown, clitellum yellow-orange with faint iridescence, ventrum pale. Prostomium closed epilobous tapering to notch that extends dorsally to 1/2 (not as far in all specimens). First dorsal pore: 5/6 faint becoming obvious by 8/9 and either obvious and continuous over clitellum or not. Setae 8 per segment from ii; lateral setal couples widely spaced; setae *a* of vi to xii seen to be damaged or dehiscent in some specimens and, on xviii *a* setae may be modified. (Samford, 1.5:1:1.5:2.2:3.3:0.30); (Brookfield, 2:1:2:2:5:0.3). Nephropores in D line 1/2-3/4, 9/10 and 11/12 then alternating, C line in 4/5-8/9, in B line 10/11, 12/13 then alternating. There is clear alternation between B and D lines for most of body length (in one Brookfield specimen the alternation was asymmetrical within segments). Clitellum raised and circular $\frac{1}{3}$ xiii, xiv-xvi, $\frac{1}{3}$ xvii (may be interrupted ventrally in xvii); furrows, setae and nephropores retained. Male pores not found. Female pores paired in xiv in common darker field antero-median to *a* setae (more closely paired in Brookfield specimens). Spermathecal pores 6/7, 7/8 and 8/9 small and concealed in furrows in B line. Genital markings none, but in two Samford specimens, tumid pads seen in *au* in x and/or xi and possibly small unpaired genital markings on xviii.

INTERNAL CHARACTERS

Septa 4/5-9/10 moderately thick, 8/9/10 the thickest, 10/11-14/15 weaker. Dorsal blood ves-

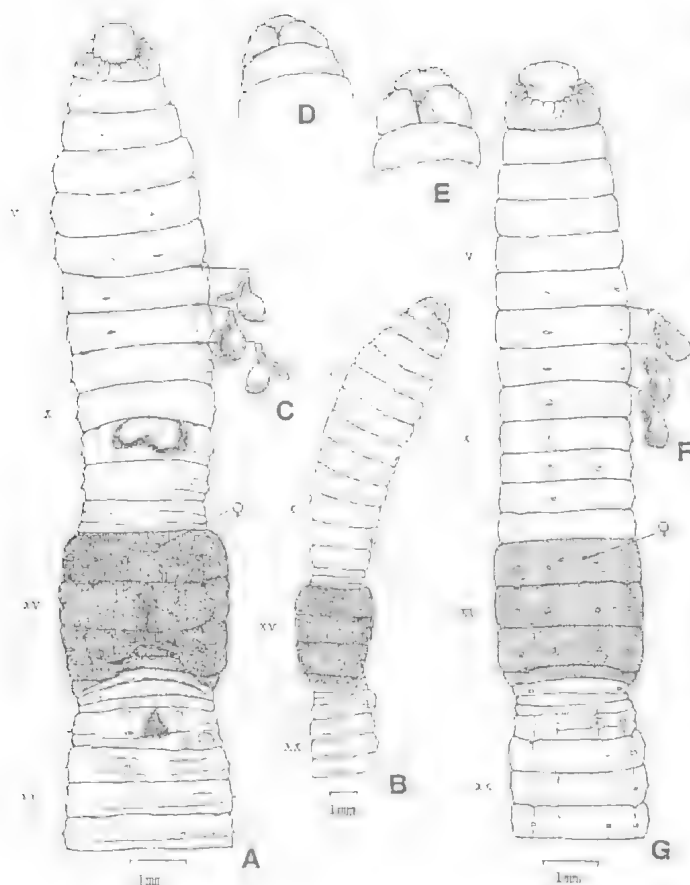


FIG. 2. *Heteroporodrilus dioecius*, Samford. A, ventral view; B, reduced lateral view; C, spermathecae; D, prostomium; E, prostomium of second specimen; G, ventral view; F, spermathecae. Prostates were aborted in all specimens.

sel single continues on pharynx. Hearts in x to xiii, commissurals in vi or vii-ix. Gizzard small and spherical, moderately muscular in v. Cal-ciferous glands 3 pairs, ventral on oesophagus in xi, xii and xiii. Intestine widening in xv, no typh-losole. Holonephridia with large bladders, seen from at least vi, alternating in position as for nephropores. Iridescent funnels of testes free, or in sacs, in x and xi, seminal vesicles in ix and xi/xii. Paired tufts of egg strings seen in xiii or in xii (this anomalous positioning was seen in two specimens from Samford). Prostates absent. Three pairs of spermathecae in vii-ix, spherical ampullae taper to ducts each with a medium length diverticulum (iridescent in several cases).

Gut contents fine colloidal material, dead roots and organic debris.

REMARKS

This species was erected on aprostatic specimens from Toowoomba (Stephenson, 1933), but Jamieson (1970) collected specimens at Petrie near Brisbane that had racemose prostates and male pores. Possibly similarly male-fertile specimens were present in the populations from which aprostatic specimens were collected in the current study, as the diverticula were in-seminated.

These specimens from Samford and Brookfield clearly lie within the descriptions of *H. dioecius*; a variation from Jamieson (1970) (apart from lack of prostates) is that the prostomium is here interpreted as being furrowed, closed epilobous rather than tanylobous. Seminal vesicles were recorded in several of these specimens in ix and xi/xii which is unusual and possibly the material filling xi was mucal coagulum. It is unusual too to observe ovaries in xii (i.e. progynous). Stephenson (1933) found in one specimen that one spermatheca, from the three pairs, was absent. Prostatic morphs of this species differ from *H. raveni* principally in having one fewer pairs of cal-

ciferous glands which are sessile rather than on short-stalks.

Heteroporodrilus doubei sp. nov. (Fig. 3)

MATERIAL EXAMINED

HOLOTYPE: QMG211897, 10km NW of Lismore, NSW, 28°48'S, 153°17'E, Dr. B. Doube, 26 Feb 1992, mature, drawn and dissected.

PARATYPES: QMG211898, mature complete; QMG211899, mature posterior amputee. Same collec-tion data as holotype.

HABITAT

In deep unstructured black clay soil-prairie podsol in deep vertical burrows in association with a *Digaster* sp. nov.

EXTERNAL CHARACTERS

Length 95-120mm. Width 3.5-4.0mm. Segments 91 (holotype) body circular. Unpigmented, transparent in alcohol. Prostomium closed epilobous. First dorsal pore 5/6, not clear on clitellum. Setae 8 per segment from ii, *ab* absent from xviii, whole length of setae can be seen through body wall after clitellum (2.13:1.0:1.63:1.75:6.0:0.36). Nephropores in D in 1/2-3/4? and 6/7 on left hand side, in C 5/6-8/9 in B in 9/10 on right hand side and 10/11 on left hand side then alternating between D and B for remainder of body. Clitellum 1/2xiii-xvii pale coloured but slightly tumid. Male pores small in site of missing *b* setae on slightly raised mound. Female pore on xiv on left hand side only (holotype) or small and paired (paratype 1). Spermathecal pores concealed in furrows 7/8/9 in B. Genital markings single, ventrally offset disc on vii; two closely paired in anterior of viii with more lateral sets in longitudinal series in line with spermathecal pores; similar discs to viii on ix except the median discs are in the setal arc; possibly the raised mounds on xviii are genital markings. Markings not as distinct in paratypes.

INTERNAL CHARACTERS

Septa 5/6 weak and finely attached to sides and base of gizzard; 6/7-10/11 moderately thickened; 11/12 on thin. Dorsal blood vessel single onto pharyngeal mass in iv. Commissurals in vi-ix; hearts in x-xiii, the last three pairs larger. Ventral vessel bifurcated under gizzard. Fine, supra-oesophageal vessel seen in xii and xiii with lateral branches. Gizzard large, muscular in v but displaced almost to 6/7. Calciferous glands small, white, ventrally sessile pairs of glands in xi-xiii. Intestine widening suddenly in xv (acaccate, atyphlosolate). Holonephridia from anterior with large, flimsy vesicles obvious in the clitellar region, alternating in position. Testis/sperm funnels iridescent, seen in x and xi but fragmented during dissection; large pairs of racemose seminal vesicles posteriorly in ix and anteriorly in xii. Ovaries not located. Prostates tubulo-racemose, confined to xviii but folded over flaccid duct. Spermathecae two pairs in viii and ix, bulbous ampullae narrow to shorter ducts, each bearing a pair of opposed clavate, iridescent diverticula. Gut contents fine soil and *Acarina* (litter mites)

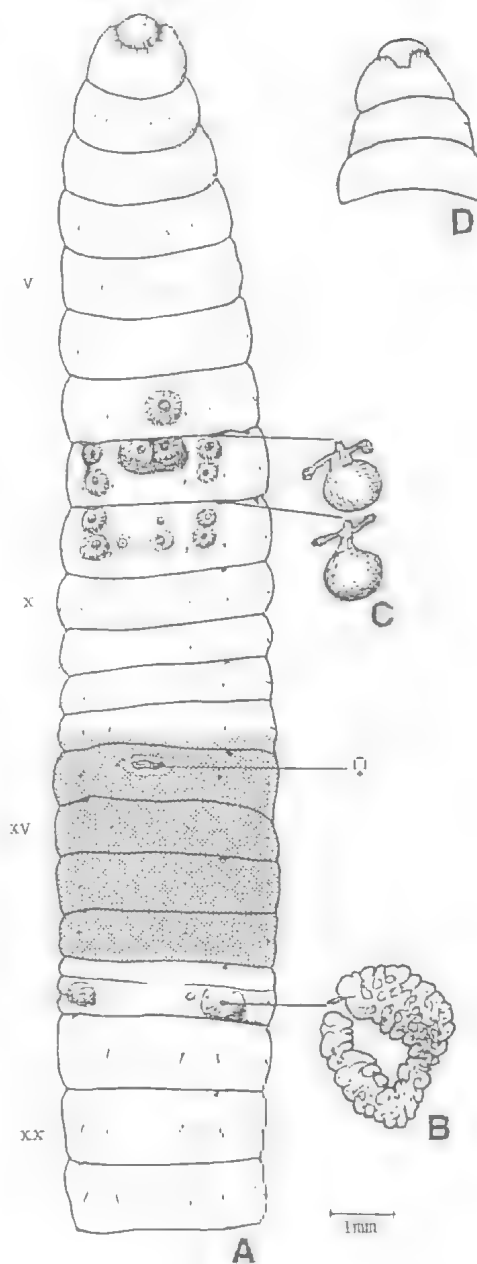


FIG. 3. *Heteroporodrilus doubei* sp. nov. A, ventral view; B, tubuloracemose prostate; C, spermathecae; D, prostomium.

suggesting geophagous/detritivores diet. Mucus invests several anterior segments.

REMARKS

Heteroporodrilus doubei has 3 pairs of calciferous glands and two pairs of bidiverticulate spermathecae, and is named after the collector. Similarities in allocation of calciferous glands and spermathecae are with *Heteroporodrilus minyoni* which, however, is much larger (400mm), and also with the bi-diverticulate *H. lamingtonensis* in which the position of the genital markings are in x and xi and xvi-xxi rather than in vii-ix.

Heteroporodrilus doubei vindicates the separation of *Heteroporodrilus s. mihi* from *Plutellus s. stricto*, outlined in the emendation of the genus above, as it has sessile calciferous glands and tubuloracemose prostates that would have bridged the previous generic definitions.

***Heteroporodrilus jamiesoni* sp. nov.**
(Fig. 4)

MATERIAL EXAMINED

HOLOTYPE: QMG211900, Mt Glorious, Qld, 27°20'S, 152°46'E, B. Jamieson collection, labelled "Or5 QSp 27", 12 Aug 1971, previously dissected mature specimen.

HABITAT

?rainforest

EXTERNAL CHARACTERS

Length 110mm (posterior amputee). Width 6mm. Segments 154+. Body spherical without dorsal canaliculation, peristomium wrinkled, preclitellar ventrum somewhat corrugated, secondary annulation slight. Unpigmented buff in alcohol, clitellum darker. Prostomium closed epilobous with distinct central cleft. First dorsal pore 6/7? wide, continuous on clitellum. Setae 8 per segment obvious from iii, *a* and *b* setae absent from xviii; lateral setal couples widely spaced (2.0:1.0:1.8:3.0:4.0:0.23). Nephropores at anterior margin of segments: ii/D, iii/D, iv/D or C, V/C, vi/C, vii/C, viii/C or D, ix/C or D, x/D, xi/B then symmetrically alternating for remainder of body. Clitellum annular $\frac{1}{3}$ xiii- $\frac{1}{2}$ xvii, interrupted ventrally in xvii. Furrows, setae and nephropores retained. Male pores on elongate porophores on xviii in B line. Female pores paired on xiv antero-median to *a* setae. Spermathecal pores five pairs 5/6-8/9 in B line. Genital markings in xvii-xx widely spaced by the width of the *a* setae, wholly presetal, laterally flattened pads which just impinge on the ventral setal couples.

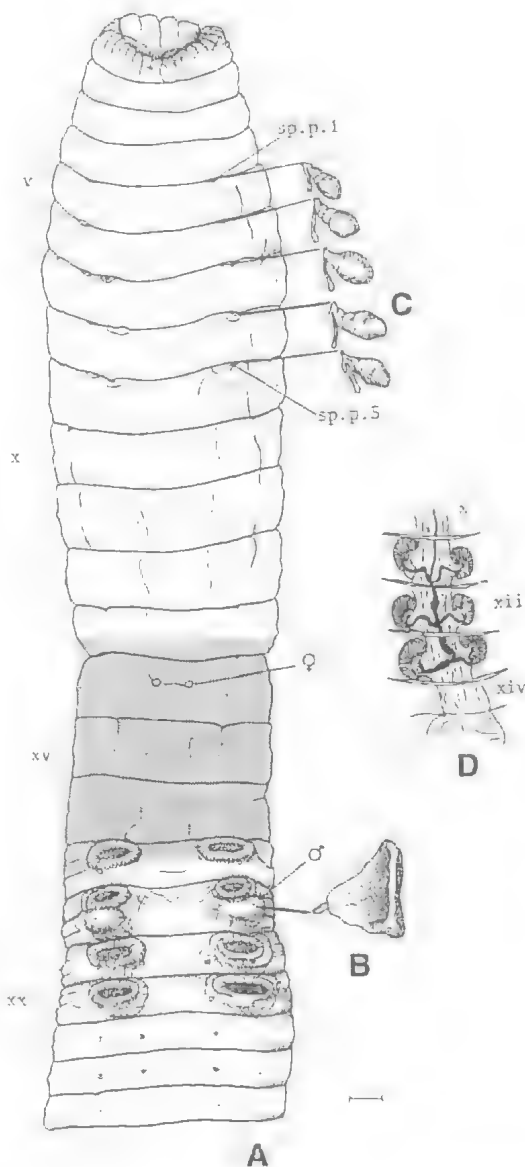


FIG. 4. *Heteroporodrilus jamiesoni* sp. nov. A, ventral view; B, prostate; C, spermathecae in situ; D, dorsal view of calciferous glands with the dorsal vessel removed. The peristomium was damaged dorsally and was not drawn.

INTERNAL CHARACTERS

Septa 5/6 weak, 6/7-12/13 becoming progressively stronger, then thinning; 5/6 and 6/7 displaced by gizzard, 10/11 and 11/12 converging and thickened. Dorsal blood vessel single con-

sinuous on pharynx. Commissurals noted in vi-ix, hearts in x-xiii. A supra-oesophageal vessel in x, strengthens from xi-xiii and, on each side, supplies the centre of each calciferous gland in these last three segments with a connective that dissipates into capillaries. (Ventral vessels not inspected). Gizzard muscular in v displacing septum 5/6 and 6/7, with wide rim anteriorly then tapering to appear cone shaped. On the oesophagus or posterior septum of vi-ix, small opalescent glands or sacs were also observed. Calciferous glands three pairs of spherical, almost reniform calciferous glands ventro-lateral to oesophagus in xi, xii, and xiii with numerous lamellae seen externally. To each gland a short stalk extends laterally from the oesophagus, and is directed downwards to the dorsal centre of each gland i.e. on short-stalks. Intestine widens in xv to reach its full width in xvi; typhlosole not found. Holonephric throughout with large convoluted tubes and flattened, round terminal bladders in the position of nephropores. Male organs holandric; especially x, but in xi too, fairly thickened pericardic (testis) sacs extend between the septa and encompass the blood vessels, oesophagus and the large iridescent funnels of the testes. Seminal vesicles are paired and racemose in ix posteriorly and xii anteriorly on septa. Ovaries small compact glands found in the anterior ventrum of xiii but individual ova not visible. Prostates compact, tongue-like, racemose glands confined to xviii each with a short, flaccid duct. Spermathecae five pairs in v-ix (the anterior pair obscured by gizzard and septa). Elongate, conical ampullae attach to tapering ducts each with a single simple digitiform diverticulum. The right side posterior diverticulum was bifid with a smaller, blunt branch. Iridescence was noted for each diverticulum. Gut contents almost entirely consisting of woody organic matter well mixed with some soil.

REMARKS

Heteropodrilus jamiesoni has three pairs of calciferous glands and five (or four) pairs of spermathecae and corresponds with Jamieson's (1970) Mt Glorious specimen he placed, despite several differences in the accounts, in *H. ashworthi* (Stephenson, 1933) (here considered a junior synonym of *H. oxleyensis*). The present specimen is especially similar with regards to the illustrations (Jamieson, 1970: figs 2; 3a; 8a,b; 9a; 10a). Differences are that only four, rather than five spermathecae were found, testis were free rather than in testis sacs as here and the ovaries and

funnels were (erroneously) recorded in xiv. Distributions of genital markings concur except for the absence in the specimen before me, of an obvious pair of presetal elliptical pads in ix and x.

This species can be separated from *H. oxleyensis* on the basis of genital markings, but not on testis sacs, which have been recorded as present or absent for both species. The spermathecae of *H. oxleyensis* and *H. jamiesoni* are similar in appearance and are recorded as 4 or 3 pairs and 5 or 4 pairs, respectively. Separating species principally on genital markings, which may vary with season or physiological or ontological state, is perhaps tenuous. But, in cases where population ranges overlap, such features are perhaps emphasised and may have a greater importance for speciation. Such small apparent variations in genital markings could be crucial deciders for mate recognition.

Of interest is that the short stalks on the calciferous glands in this specimen are similar to those for *H. oxleyensis* (Mt Cotton specimen) as well as those illustrated for *Heteropodrilus minyoni* comb. nov. (Dyne, 1980: fig. 2b).

Heteropodrilus oxleyensis (Fletcher, 1889) (Figs 5, 6)

MATERIAL EXAMINED

QMG210140, 2 mature, dissected specimens, Lower Savages Rd., Brookfield (27°30'S, 152°55'E), early mornings, C.H. Thompson, 17 May 1992; 1 mature specimen, same locality data as previous, 31 Dec 1992, author's collection; QMG210141, 1 mature specimen (with the posterior amputated but retained) and three sub-adult and two immature specimens, Queensland University farm, Mt Cotton (27°53'S, 153°14'E), R.J. Blakemore, S. Jeffries, 19 Jan 1993; sub-adult specimens, same collection data as previous, A. Wilkie, Aug & Oct, 1992, author's collection; one mature specimen, possibly a posterior amputee, Samford CSIRO farm (27°22'S, 152°53'E), R.J. Blakemore, V.R. Catchpole, 5 Feb 1992, author's collection. Descriptions following are in the same order as the three locations.

HABITAT

On road near remnant rainforest: under 'blue gum' (*Eucalyptus tereticornis*) and *Leucaena leucocipha* plantation, particularly in red podsollic soil; under grass in a non-calcic brown soil.

EXTERNAL CHARACTERS

Length of mature specimens: 100-120mm; 140mm; >92mm (less mature specimens: 33-110mm). Width of larger specimens: 5.5-6mm; 4mm; 5mm. Segments of mature specimens:

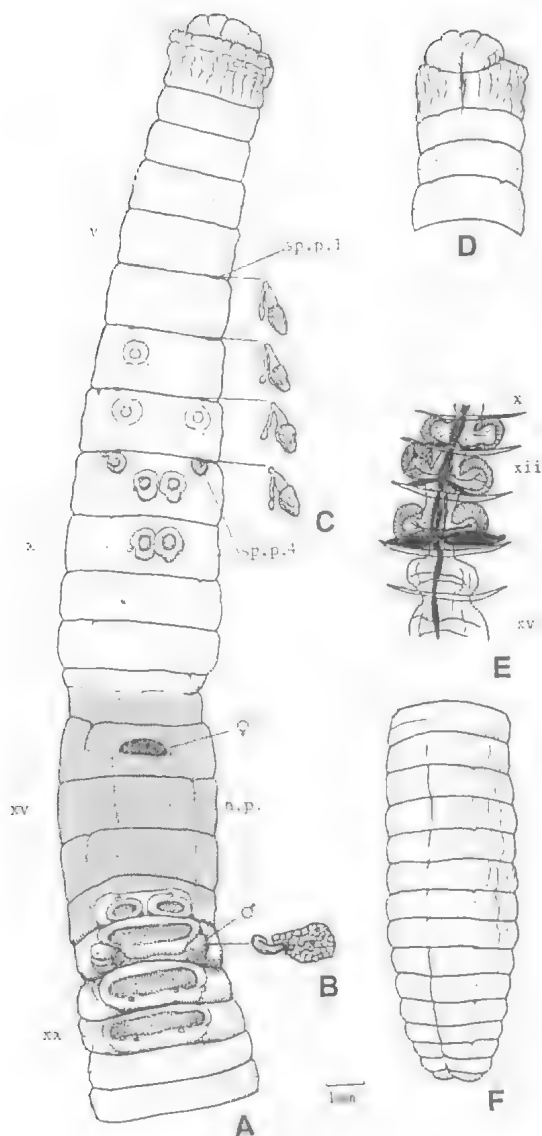


FIG. 5. *Heteroporodrilus oxleyensis*, Mt Cotton, mature specimen. A, ventral view; B, prostome; C, spermathecae in situ; D-F, dorsal views. D, prostomium; E, calciferous glands; F, posterior.

161, 185, 190; 167; >119 (others: 113-159). Secondary annulation minimal. Slight dorsal furrows in caudal segments. Colour of dorsum, especially in anterior and caudal segments, pigmented light yellowish-brown with slight iridescence (Samford specimen dark grey), ventrum pale; clitellum buff. Prostomium closed epilobous with

distinct dorsal cleft extending from tip of prostomium through to 1/2 or 2/3 (seen in all larger specimens). Immature specimens have furrow to 1/2 only but short grooves also flare from prostomial junction. Pharynx may evert on preservation. Peristomium usually rugose. First dorsal pore 5/6 faint, 6/7 wide; 6/7 rudimentary, from 7/8 distinct; obvious from 7/8. Setae 8 per segment from ii, *a* and *b* (always?) absent from xviii; lateral setal couples widely spaced, (2:1:2:2:4:3:0.27); (2.0:1.0:2.0:2.3:3.7:0.23); (2:1:2:2:3:0.3). Nephropores in D line 1/2-3/4, 5/6 or 6/7, then alternating; in C line, when not in D in 4/5-7/8 and alternating in B line from 9/10. Clear alternation between B and D lines for remainder of body. In some specimens,

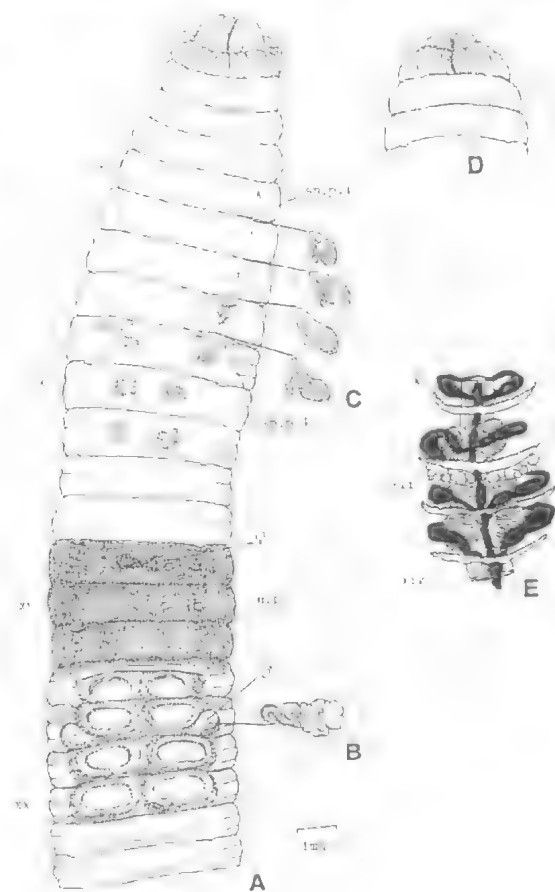


FIG. 6. *Heteroporodrilus oxleyensis*, Samford specimen. A, ventral view; B, prostome; C, spermathecae; D, prostomium; E, ventral view of calciferous glands.

nephropore alternations were asymmetrical in B and D per side. Clitellum $\frac{1}{2}$ xiii- $\frac{2}{3}$ xvii, xvii interrupted ventrally in xvii; setae, nephropores, furrows and dorsal pores retained. Male pores on xviii on slightly raised porophores, approximately in B line (on immature and subadult specimens seen within small lateral creases). Female pores on xiv a pair anterior-medial to a setae in common darker lateral patch. Spermathecal pores four pairs in 5/6-8/9 in furrows in B line. Genital markings of Brookfield specimens: in some of vi-xi small closely paired, median pads, in xvii closely paired or elongate postsetal pads, xviii-xx (and xxi in one unusual specimen) tumid, elongate, mostly presetal pads; Mt Cotton: in vii and viii single or paired faint discs anterior to ventral setal couples, in ix and x closely paired discs between *a* setae, also in ix a smaller pair of markings just behind the spermathecal pores, in xvii a pair of postsetal pads, closely paired in common ventral tumid area and mostly presetal in each of xviii-xx: elongate smooth pads sunken in otherwise raised glandular areas; Samford: in ix-xi small, ventrally paired discs, in xvii postsetally and presetal in xviii-xx large, paired pads elongate from mid-ventrum to B lines.

INTERNAL CHARACTERS

Septa 4/5 membranous to anterior of gizzard, 5/6 thin and much displaced to accommodate gizzard, 6/7-11/12 only slight, but progressive thickening, 12/13-14/15 thinning and thereafter membranous. Septa 4/5-8/9 are posteriorly displaced to a lessening degree, 9/10 and 10/11 are adherent. Pharyngeal tendons extend through anterior septa. Dorsal blood vessel single continuous onto pharynx. Commissurals from vi-x, hearts in xi-xiii. In Mt Cotton specimens: supraoesophageal vessel not found in xi but developed in xii and xiii with small connective to dorsal heart valves and lateral branches attached to stout pink stalks that pass to dorsal centres of the calciferous glands on each side. The hearts pass to ventral vessel, dorsal to which is a separate vessel that seems to supply the calciferous glands at their ventral axes. The dorsal vessel from xiv has two small pairs of vessels in each segment that pass to each side of the alimentary canal. Gizzard tubular to spherical and muscular in v. Calciferous glands three pairs in xi, xii, and xiii: spherical glands with white lamellae in section and visible externally, lay ventro-lateral to the oesophagus on short stalks (in one Brookfield specimen the glands are anomalous in xi then in

xiv and xv on left side only). Intestine widening through xv; no typhlosome. Nephridia paired holonephridia with long convoluted tubes and deflated, subspherical to elongate, terminal bladders, from at least v, corresponding in position to the nephropores. Iridescent testes and funnels ventrally in x and xi within pericardic testis sacs (strong in x, more membranous in xi); a small pair of racemose seminal vesicles posteriorly on septa in ix (and xi) and (lobulate) anteriorly in xii. A compact pair of glandular ovaries (individual ova not discernible) in anterior and nebulous oviducts in posterior of xiii. Prostates paired racemose glands, confined to xviii each with a short, ensheathed duct bent in single loop. Spermathecae four pairs in vi-ix; conical, flecked ampullae connect to tapering ducts each with a single diverticulum. Iridescent (inseminated) diverticula only noted in Samford specimen. Gut contents mostly organic matter including woody (dead root) material, plus some fine and some coarser soil.

REMARKS

Despite some variation between the specimens described above from the three locations, it was decided to include this new material in *H. oxleyensis*. The original brief description by Fletcher (1889) was based on one acitellate specimen (plus two incomplete specimens). Subadult specimens from Mt Cotton differ insubstantially from this original description apart from having about 15-20 fewer segments. Moreover, the mature specimens from Mt Cotton and the other two locations above agree sufficiently with each other and with Stephenson's (1933) single specimen of *Woodwardiella ashworthi*, here regarded as a junior synonym of *H. oxleyensis*.

Justification for this synonymy is that Stephenson (1933) omitted to refer to the earlier description, yet his specimen from Brisbane agrees on every point in common with Fletcher's (1889) *H. oxleyensis* apart from those attributable to its being mature. The only other records of *H. oxleyensis* are the two specimens (from Kholo Creek and Marrickville) described and illustrated by Jamieson (1970). These also concur with Stephenson's (1933) specimen except that they are slightly truncated, have dorsal pores in 5/6 or 6/7 (rather than 7/8), do not retain setae *a* of xviii, one has three pairs of spermathecae (rather than four) and they have paired postsetal genital markings in xvii (rather than an analogue, Stephenson, 1933: fig. 12).

***Heteroporodrilus thompsoni* sp. nov.**
(Fig. 7)

MATERIAL EXAMINED

HOLOTYPE: QMG210142, Lower Savages Rd. and near Gold Creek, Brookfield, Qld (27°30'S, 152°55'E), C. H. Thompson, 08 Apr 1992.

PARATYPES: 6 specimens, QMG210143- G210146, same collection data as holotype, 15 Apr 1992, 17 May 1992, 30 Dec 1992.

HABITAT

Under leaf litter of rain-forest and eucalypt woodland and on road surface, especially after rain.

EXTERNAL CHARACTERS

Length 210-270mm (holotype: 210mm, but some damage to middle area). Mass 21.5g(holotype). Width (midclitellar) 11-13mm. Segments 181-235, (holotype 235). Faint secondary annulation, especially after the clitellum. One specimen had marked dorsal furrow (i.e. canaliculate) in the latter half of its body. Unpigmented, grey in alcohol; clitellum darker pink-grey and faintly iridescent. Prostomium closed epilobous to pro-epilobous with definite furrow that bisects prostomium and extends to 2/3 as a groove. Peris-

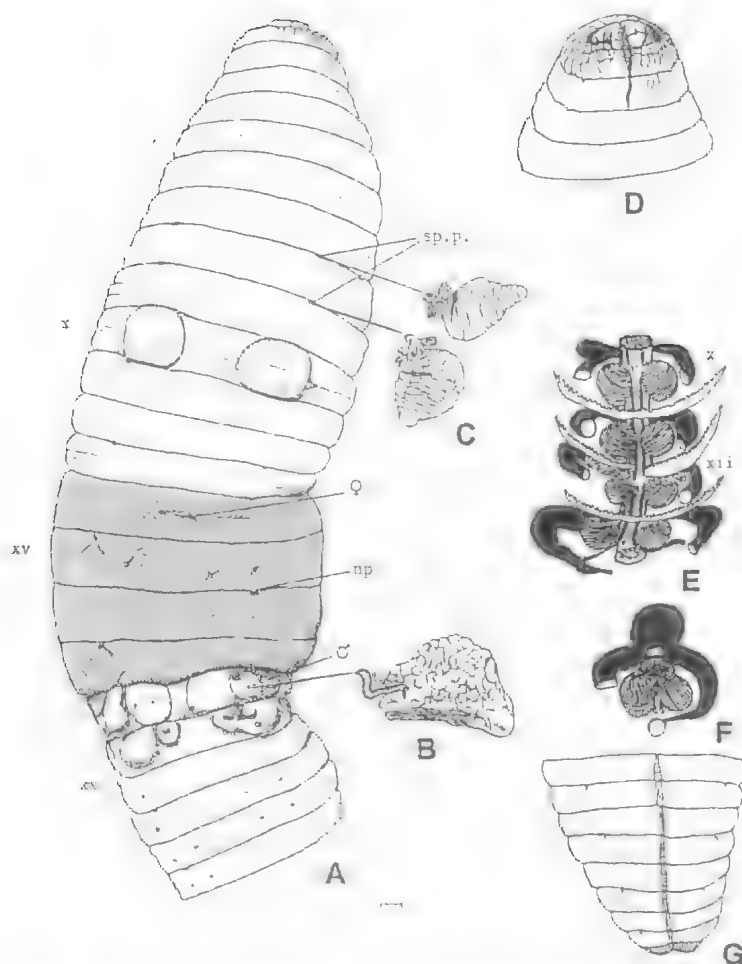


FIG. 7. *Heteroporodrilus thompsoni*. A, ventral view of paratype; B, prostate; C, spermathecae in situ; D, dorsal view of prostomium; E, ventral view of calciferous glands with ventral vessel cut away; F, anterior view of calciferous glands from xiii with left-side sectioned; G, posterior.

Confusion over the definition of *H. oxleyensis* that resulted mainly from its designation on sub-adult material (as was *H. sloanei*, also by Fletcher, 1889) has been reduced by this revision. The combination of three pairs of calciferous glands in xi-xiii (mislabelled in Jamieson, 1970: figs. 3d, 5g as in ix), four (or three) pairs of spermathecae and postsetal genital markings in xvii are unique to this species. The distribution in the Brisbane region of southeast Qld. is dissipated only by the one anomalous record from the suburb of Marrickville, Sydney, NSW (collector M.E. Grey, 1933).

tomium rugose. First dorsal pore not clearly detectable in deep furrows but seen in 10/11 and 13/14 at least, and again from 17/18. Setae 8 per segment, from ii, dark tipped, *ab* absent from xviii (mean of four specimens; 1.7:1.0:1.5:2.5:3.8:0.26). Nephropores at anterior margin of segment almost in furrow, obvious on clitellum. The most common arrangements: ii/D, iii/D, iv/C or D, V/C, vi/C, vii/C, viii/C or D, ix/D or C, x/B, xi/D, xii/B, xiii/D, xiv/B, xv/D, xvi/B, xviii/D, xviii/B, xix/D, xx/B, xxi/D, etc. Several specimens had irregular pore distributions to the above scheme, one had the opposite arrangement from x,

another two had asymmetrical alternations within a segment (i.e. a pore in B and one in D). Clitellum annular and tumid xiv-xvii, setae and nephropores retained often in deep dimples. Male pores in xviii in site of *b* setae on slightly raised porophore. Female pores on xiv variously closely paired antero-medial to *aa*, sometimes concealed in a lateral groove, alternatively a single pore on a slightly tumid pad antero-medial to *aa* setae. Spermathecal pores two pairs in 7/8 and 8/9 almost hidden in furrows in B line but visible under traction. Genital markings in x in all specimens: a distinct pair of circular, tumid pads occupying the longitudinal width of the segment and encompassing the ventral setal pairs. In xviii, the areas of the missing ventral setal couples are generally tumid with a mid-ventral hollow and in xix is a similar glandular area which extends as far as the limit of the ventral setae.

INTERNAL CHARACTERS

Septa 4/5-7/8 moderately thickened, 8/9-12/13 becoming progressively much thicker, then, after 13/14, thinning. Dorsal blood vessel single, continuous on pharynx. Commissurals in vii-ix, large hearts in x-xiii. From ix or x to xiv or xv large bladders dominate the dorsal vessels, in xv the enlarged dorsal vessel has two pairs of ventrally directed vessels which surround the oesophageal valve. Bifurcate ventral blood vessels form a pair of hairpin loops under gizzard before moving anteriorly. Gizzard large, muscular and barrel shaped in v with slight anterior rim, compressing septa 5/6 onto 6/7 and reaching as far back as vii. Calciferous glands four pairs in x-xiii, the anterior pair the smallest, as spherical, white, ventral pouches sessile on oesophagus each with numerous fine lamellae internally. A pair of sub-oesophageal blood vessels run between the lobes of each pair of glands. Intestine origin abrupt in xv or xvi, no typhlosole. Holonephric, with large, subspherical to elongate, flattened bladders corresponding in position with external nephropores. Male organs holandric: large paired, iridescent funnels of testes free (or appearing in testis sacs in at least two specimens) in x and xi. Seminal vesicles medium to small size, paired and racemose in ix and xii (the latter lobulated on anterior septum). In ix white coagulum, the same texture as in seminal vesicles, frequently seen. Ovaries as a small pair of egg-string tufts anteriorly in xiii and paired diaphanous oviducts on posterior ventrum. Prostates con-

fined to xviii, a pair of compact, squarish, racemose glands with short, bent duct joined entally by vasa deferentia. In section the prostates appear solid without obvious central lumina. Spermathecae two pairs in viii and ix: large bulbous but slightly deflated or deflected subspherical ampullae with fine concertina-like corrugations, attach to shortish ducts bearing several (two to six), small digitiform or bi-, tri-, or multi-lobed diverticula encircling the duct near the ectal end. Stalks (and occasionally termina) of several diverticula have lustre indicating insemination. Gut contents mostly reddish silt with some grits and sometimes organic debris including woody remains (geophagous/detritivorous).

REMARKS

The combinations of four pairs of calciferous glands and two pairs of polydiverticulate spermathecae identify *H. thompsoni* which is named after the collector. This species has close affinities with the similarly large *H. tryoni*, also collected from this location. It differs from *H. tryoni* in having one fewer pair of calciferous glands, one fewer pair of spermathecae, different setal ratios and in having a distinct pair of genital markings in x. *H. tryoni* usually has a pair or trio of tortuous diverticula on each of its three pairs of spermathecae, often with sessile seminal chambers. It is noteworthy that Boardman's (1932) description for *H. youngi* (syn. *H. tryoni*) has compound diverticula similar to those described here for *H. thompsoni*, but here again there are three pairs of spermathecae (even in his paratype where he reports only dissecting the first two spermathecae from segment vii and viii).

Heteropodrilus tryoni (Fletcher, 1889) (Fig. 8)

MATERIAL EXAMINED

QMG210147, Adayale St and Lower Savages Rd, Brookfield, Qld. (27°30'S, 152°55'E), C.H. Thompson, 8 Apr 1992, one damaged mature specimen dissected and drawn; QMG210148, 17 May 1992, one intact specimen; QMG210149, 26 May 1992, two damaged specimens dissected.

HABITAT

Under litter, on surface after rains and at about 30 cm depth in a deep surfaced eucrozem soil with clay-loam surface texture (field pH 6.0).

EXTERNAL CHARACTERS

Length 270-300mm. Mass 35.85g (damaged but complete specimen). Width (midclitellar) 14-17mm. Segments: 235-236. Peristomium wrinkled, second segment less so. Marked dorsal furrow in latter part of body. Pigmented dorsum dark grey in alcohol; clitellum slightly darker with faint green tinge. Prostomium closed epilobous to pro-epilobous with definite furrow that bisects prostomium and extends to 2/3 as a groove. First dorsal pore in 6/7 or 7/8. Setae small, 8 per segment from ii, ventral setal couples widely spaced; ventral setae absent on xviii. (mean; 2.0:1.0:1.8:3.5:4.3:0.24). Nephropores at anterior margin of segment in furrow, irregular alterations noted for two specimens: ii/DD, iii/DD, iv/DD, v/CC, vi/DB, vii/CD, viii/DC, ix/CD, x/DC, xi/CD, xii/DB, xiii/BD, xiv/DB, xv/BD, xvi/DB, xvii/BD, xviii/DB, xix/BD, xx/DB, xxi/BD this alternation continued for the remainder of the bodies. Nephropores do not open in B lines in vii, viii nor ix as these positions are occupied by the spermathecal pores. Clitellum annular and tumid; 1/2xiii, xiv-xvii but interrupted ventrally on xvii by genital markings. Setae and nephropores retained. Male pores paired in xviii on small circular porophores at centre of generally tumid patch centred at site of aborted *b* setae. Female pores on xiv in lateral groove stretching between *a* setae, but just anterior to setal arc. Spermathecal pores in 6/7, 7/8 and 8/9 almost hidden in furrows in B line but visible under traction as minute pores. Accessory genital markings in x and xi slightly raised pair of tumid pads filling the anterior aspects and just incorporating the ventral setal pairs; in xvii a pair of sucker-like markings with the ventral setae in the lower edge; in xix a similar pair of pads although possibly slightly wider.

INTERNAL CHARACTERS

Septa 5/6 and 6/7 weak but adpressed, 7/8-12/13 thick, 13/14 moderately thick, thereafter membranous. Dorsal blood vessel: single and considerable. Commissurals in vii-ix, large hearts in x-xiii. Gizzard moderately muscular and cone shaped in v with wider anterior rim. Calciferous glands five pairs in ix-xiii, the anterior pair the smallest, as spherical, white, ventral pouches sessile on oesophagus each with numerous fine lamellae internally. Intestine origin in xv, no typhlosole. Holonephridia with largish, subspherical collapsed bladders in position of external



FIG. 8. *Heteroporodrilus tryoni*. A, ventral view of an anteriorly damaged specimen; B, prostate gland; C, spermathecae in situ; D, enlargement of a spermathecae.

nephropores. Iridescent funnels of testes free in x and xi close to ventral nerve cord. Seminal vesicles small and racemose in ix and xii. Ovaries as tufted strings in xiii with paired egg funnels on posterior ventrum. Prostates confined to xviii, a pair of tongue-like racemose glands with thin, straight, non-muscular duct. Spermathecae three pairs in vii, viii and ix: constricted, bulbous ampullae narrow abruptly to ducts bearing ventrally, three medium-sized, tortuous diverticula. The central diverticulum in each case was the most convoluted. Iridescence was seen in all diverticula. The same grey coagulum as was found in the body cavity reappeared in the gut. The ingesta was mainly dead plant remains including large woody husks and small leaf skeletons.

REMARKS

These large specimens are identified as *H. tryoni* having five pairs of calciferous glands and three pairs of poly-diverticulate spermathecae.

The present description consolidates that of Jamieson (1970) as the specimens here described appear to have intermediate characters within the range of the earlier species description. The form is intermediate to the two heteromorphic specimens illustrated in the previous account (Jamieson, 1970: figs. 5b, 5c). *H. tryoni* appears closely related to, but discrete from, the sympatric *H. thompsoni*.

Plutellus

Perrier, 1873 emend.

TYPE SPECIES

Plutellus heteroporus Perrier, 1873 nf
(presumably) Australian origin in NSW.

REMARKS

The generic description largely reverts to that of Jamieson (1971a), combined with features of the single Lord Howe Island species, *P. hutchingsae* Jamieson, 1977 (as shown in the brackets in the following diagnosis).

DIAGNOSIS

Small to moderately large terrestrial worms. Prostomium tanylobous (or epilobous). Combined pores of a pair of tubular (or 'thickly tubular') prostates and male pores in xviii. Spermathecal pores 4 or 5 pairs, the last in 8/9 in B lines (A lines), 8 setae per segment. Holonephric with large nephridial bladders; anterior nephropores in C or D lines and, from v-vii posteriorly, alternating from D to B lines. Gizzard, strong in v. Last heart xii (xiii). Four pairs of long-stalked i.e. better than twice as long as broad, reniform calciferous glands in x-xiii. Holandric. Gymnorchous. Spermathecae monodiverticulate.

DISTRIBUTION

Restricted to the central coastal region of New South Wales; Lord Howe Island.

SPECIES OF *PLUTELLUS*

1. *Plutellus heteroporus* Perrier, 1873.
Plutellus heteroporus Perrier, 1873: 245-268, figs 1-3; Beddard, 1895: 487; Michaelsen, 1900: 174; Jamieson, 1971a: 1300-1310, fig. 1 (portions of type species).
2. *P. hutchingsae* Jamieson, 1977: 276-277, figs. 1; 2b; 6h; 7e-i; from Lord Howe Island.

3. *P. manifestus* (Fletcher, 1889) from Audley National Park and Bulli, NSW.
Cryptodrilus manifestus Fletcher, 1889: 1538-1539, (seven specimens); Buchanan, 1910: 215-216, figs 4, 7.
Platellus manifestus; Michaelsen, 1900: 173; Jamieson, 1970: 129-132, figs 6a, b; 8e, f; 9h; (eleven clitellate and some acitellate specimens).

SPECIES INQUIRENDUM

Plutellus rubens (Fletcher, 1887), from Mt Wilson, NSW.

Cryptodrilus rubens Fletcher, 1887a: 381-383, (a few small spirit specimens)

Megascolides rubens; Beddard, 1895.

Plutellus rubens; Michaelsen, 1900.

Note: Fletcher conceded that spermathecal and nephridial pores were not visible in this holonephric species with "long narrow" prostates, although four pairs of calciferous glands were recorded in x-xiii and the last heart in xii. He went on to remark that the spermathecae and gizzard may have been overlooked for this small (55mm) species. This imperfect characterization has not subsequently been corroborated.

KEY TO *PLUTELLUS*

- | | |
|---|-----------------------|
| 1. 5 pairs of spermathecal pores, at anterior margins of v-ix | 2 |
| 4 pairs of spermathecal pores, at anterior margins of vi-ix, almost contiguous midventrally | <i>P. manifestus</i> |
| 2. Spermathecal pores in B lines. Last hearts in xii | <i>P. heteroporus</i> |
| Spermathecal pores in A lines. Last hearts in xiii | <i>P. hutchingsae</i> |

Plutellus heteroporus Perrier, 1873

(Fig. 9)

MATERIAL EXAMINED

Port Macquarie, NSW (31°27'S, 152°55'E), B.G.M. Jamieson collection: 2 specimens (mixed with species of several other native genera): one acitellate, one posterior amputee at 16/17; both drawn and described here, 8 miles from Beechwood on Bellangry and Wilson River St, Forest Rd. Riverine forest sloping into gully, black soil under logs and in earth, W. Nash, R. Raven, 17 Jul 1975; 5 specimens tagged PH1 - PH5 (PH1 dissected, PH2 drawn, other specimens inspected), near Cairncross State Forest, 6.4km S of Telegraph Point turnoff by Pacific Hwy. Wet black soil in paperbark and tea tree swamp, W. Nash, R. Raven, 16 Jul 1975.

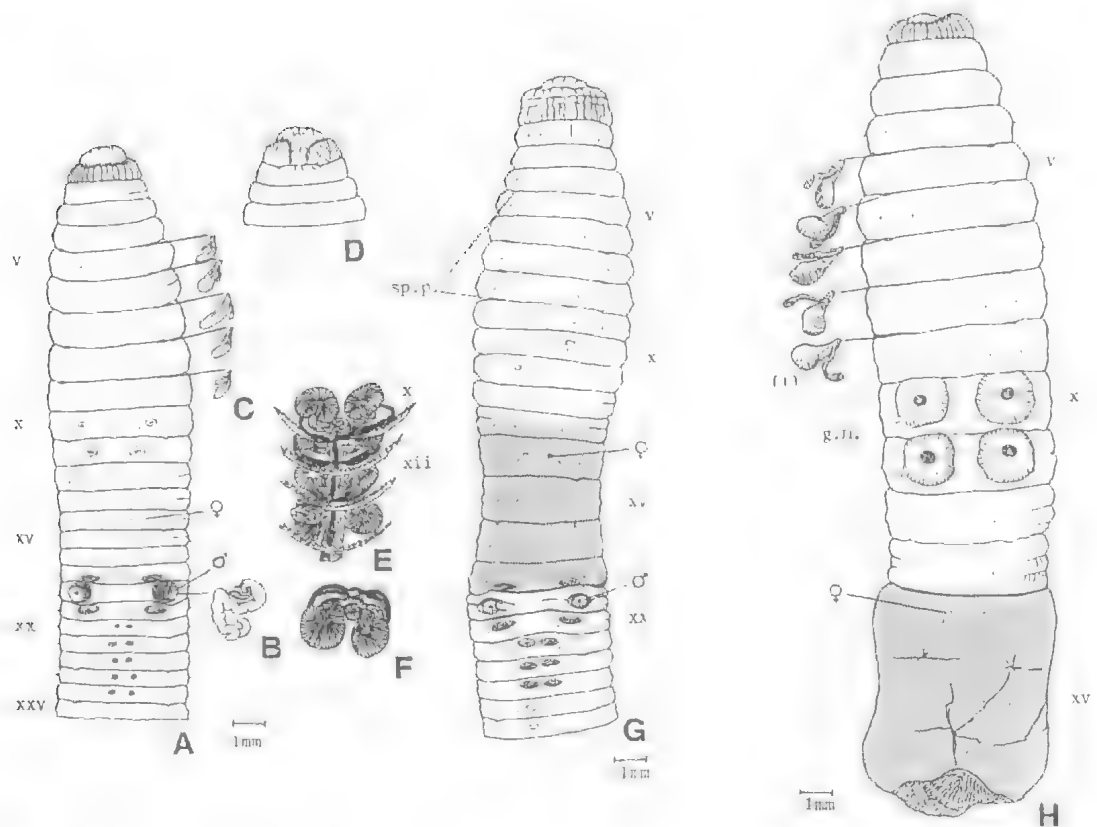


FIG. 9. *Plutellus heteroporus*. A, ventral view of acitellate specimen; B, tubular prostate; C, spermathecae; D, prostomium; E, dorsal view of calciferous glands in situ; F, anterior view of calciferous glands of xiii showing long ducts beneath lateral hearts; G, ventral view of specimen PH2; H, ventral view of posterior amputee specimen; I, spermathecae in situ (prostates lost).

EXTERNAL CHARACTERS

Length 77-175mm. Width 4-5mm. Segments 185-209. Body circular in section with secondary annulation dorsal from x and in post-clitellar segments. Pigmentless buff in alcohol, not iridescent, clitella manilla. Setal lines appear darker in some specimens. Prostomium tanylobous. First dorsal pore 7/8. Setae, especially ventral couples, dark, 8 per segment from ii, *a* and *b* absent from xviii, (mean of three setal ratios, 1.7:1.0:2.3:2.1:2.9:0.2). Nephropores paired in D line 1/2, 7/8, 9/10, 11/12, 13/14, 15/16, 17/18, etc.; in C line 2/3, 3/4, 4/5, 5/6 (one specimen in 6/7 too, another specimen in 8/9 also); in B line 6/7?, 8/9, 10/11, 12/13, 14/15, 16/17, 18/19, etc. One specimen had irregular alternations, but mostly alternation between D and B in successive segments. Clitellum $1/3$ xiii(dorsally), xiv-xvii annular, setae and nephropores retained, intersegmental furrows faint, dorsal pores occluded. Male

pores minute in xviii on small raised porophores in B line, each within a smooth, flattened, sub-spherical dish that fills the segment longitudinally. Female pores in xiv a minute pair widely spaced but antero-medial to *a* setae. Spermathecal pores five pairs in B lines from 4/5 - 8/9. Accessory genital markings in one specimen, a pair of large but lowset presetal pads with darker centres between *ab* in x and xi extending from the setal arc to the anterior furrow. In other specimens, these marks were not clearly defined but a similar pair of pads were present in one in xi, on the left side only in one and in xii in another. Postsetally in xvii, a pair of ellipsoid smooth dishes between *ab* with translucent centres and shelving towards xviii; in xix a similar pair of marks presetally. Ellipsoid dishes, presetal, closely paired (occasionally single) and ventral to *aa* also present in each specimen in some of xx-xxiv (commonly in xx-xxii).

INTERNAL CHARACTERS

Septa 4/5 membranous, 5/6–12/13 moderately thickened (especially the first three impinging rearwards), 13/14 and 14/15 thinner, then membranous. Dorsal blood vessel single continues on pharynx. Commissurals vi–ix, larger hearts in x–xii. Gizzard thin walled but muscular in v, tubular or tapering. Calciferous glands four pairs laterally in x, xi, xii and xiii; rosette or reniform with radiating lamellae attaching to the oesophagus dorso-laterally via long curved ducts, one from each gland. Ducts well supplied with blood capillaries and originate near the centre of each gland. The glands are solid and consist of numerous internal lamellae. Oesophagus narrows in xiv (valve?) then widens in xv as intestine proper; in xv and xvi it is especially dilated; typhlosole and caeca not seen. Holonephric from ii. Large elongate bladders are associated with the nephropores i.e. they have alternate extensions in successive segments for most of the body. Iridescent funnels of testes free in x and xi; racemose seminal vesicles occupy ix and xii. Ovaries paired ventrally in xiii, numerous egg strings are loosely attached to give fan-like appearance. Prostates a pair of elongate and tortuous tubular prostates (internal lumina not visible) overlaying short muscular ducts (dilated near body wall) in xviii. The prostates extend from xviii to xix (one abnormal specimen had a continuation of the gland directed forwards as far as xvi). Spermathecae five pairs in v–ix; elongate ampullae taper to narrowing ducts each bearing a single clavate diverticulum on stalks almost as long as ampulla (in mature specimens the diverticular bulbs were iridescent). Gut contents colloidal dark soil with no obvious organic debris.

REMARKS

The above specimens correspond with previous descriptions of the type-series of the genus *Plutellus*, in particular that of Jamieson (1971a). Additional features recorded here are the first nepridiopores in D line in 1/2, new body dimensions, segmental counts, setal ratios and accessory genital markings. Large ventral disks in x and xi developed in one specimen resemble those seen in *P. manifestus* (see Jamieson, 1970: fig 6a). New illustrations are provided.

Plutellus heteroporus has very close affinities with *P. manifestus* from NSW and *P. hutchingsae* from Lord Howe Island, not least in having tubular prostates. Characteristics of the genus are the alternation of nephropores and, separating it from both the allied Australian genera

Heteropodrilus and the monotypic Lord Howe Island *Paraplutellus* Jamieson, 1972 (see Jamieson, 1977) the possession of four pairs of clearly stalked calciferous glands.

Jamieson (1971a), related how two lots of specimens were mixed in the same bottle in the Paris museum where Perrier first described type material in 1873. At about the same time, *Digaster lumbricoides* Perrier, 1872 was erected from specimens collected at Port Macquarie in 1846 (by M. Le Souef?). It is significant that this locality is the same as for the *P. heteroporus* specimens described above. The provenance of this new material then, supports the probable type-locality as being in Australia, and in particular Port Macquarie NSW, rather than Pennsylvania, (USA) as was presumed by Perrier.

DISCUSSION

Plutellus clearly retains the more 'primitive' tubular form of prostates, *Heteropodrilus* is thus considered an apomorphic sibling-group of *Plutellus* that has reached a climax in rainforest and riverine environments in the Qld. subtropics. This view contrasts with that of Dyne (1981: 105) who considered sessile calciferous glands as a plesiomorphic condition and the stalk-glanded *Plutellus* as the more derived genus.

Evidence that *Heteropodrilus* has diversified in south-east Qld. is provided here by surveys that have located four of the six previously described species for this region, and added several more to the list. One small area at Brookfield in Brisbane has yielded four species in association: *H. tryoni*, *H. thompsoni*, *H. dioecius*, *H. oxleyensis*, often in the same sample. If the origin of the genus is taken to be south-east Qld., then the focus of endemicity (as indicated by the abundance and diversity of species and specimens) may well be in the catchments and rainforest foothills of the D'Aguilar Range of which Mt Glorious is a high point. Nevertheless, the diversity of *Heteropodrilus* species around Brisbane may be an aberration of sampling effort especially as much of the inland areas of the eastern sub-region have yet to be systematically sampled and are expected to provide further species. A fuller picture of the biogeography, as with the systematics of these and other species, may await genetic analyses.

That the types of *H. dioecius* were from Toowoomba on the Great Dividing Range demonstrate that this escarpment is no barrier to heteropodrilid migration. Another species,

H. bongeen, was recorded from the Condamine River plain west of Toowoomba in the Darling Downs region. This river, which at one time may have united with the Burnett River, eventually connects with the Murray-Darling river systems of New South Wales, Victoria and South Australia where distributions of other *Heteropodrilus* spp. have been recorded. The riverine transport mechanism for this genus is thus supported. The propensity for nocturnal or crepuscular wanderings (particularly after flooding?), noted for several species above, may further enhance their ability to disperse.

Several members of this genus are associated with riparian habitats where their burrows can easily access the water-table, they may thus survive apparently dry conditions. Osmotic regulation and secretion via large, exonephric terminal bladders, are perhaps enhanced by nephrophore alternation. Possibly this adaptation serves partly to maintain a more even body surface moisture, for respiration, lubrication and defence, especially in worms with larger surface areas, than would a regular series of nephropores. Both *Plutellus* and *Heteropodrilus* contain medium to large sized members. However, alternation of nephropores is found in other genera too eg. *Maoridrilus* Michaelsen, 1899, from New Zealand and in at least one member of the Australian native *Diplotrema* (*D. heteropora* Dyne, 1979).

ACKNOWLEDGEMENTS

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PIGMENTATION BANDS ON AN EARLY DEVONIAN NAUTILOID. *Memoirs of the Queensland Museum* 37(1): 40, 1994:- A specimen of an ?orthoceratid nautiloid was collected in 1990 from the Martins Well Limestone, Broken River Province, north Queensland (QM Locality 549). The Martins Well Limestone member of the Shield Creek Formation contains a diverse fauna indicative of an Early Devonian (Lochkovian- Pragian) age (Jell et al., 1993). The specimen (QMF32208) is a 92mm long fragment of an orthoconic shell (Fig. 1) and is exposed only on the lateral parts of the shell with the dorsum and venter apparently obscured. The shell had been encrusted by an actinostromatid stromatoporoid skeleton, and the preserved shell surface represents this encrusted surface.

Upon the outer shell surface are preserved thin, light grey sinuous bands 1.8-2.0mm thick, separated by thicker dark grey bands 3.3-4.4mm thick. The pattern is restricted to the exterior shell surface, and the pigmentation does not appear in longitudinal section as sutures or septal remnants. Ribbing is discounted given that a longitudinal section revealed a thin smooth, un-ribbed shell. The pattern is thus considered as a relict surface pigmentation.

Preservation of pigmentation patterns on Palaeozoic cephalopods is rare (Foerste, 1930; Teichert, 1964). Preserva-

tion, in this case appears to have been facilitated by the early encrustation of the stromatoporoid, providing protection against crushing, and a significant buffer to destructive diagenetic processes.

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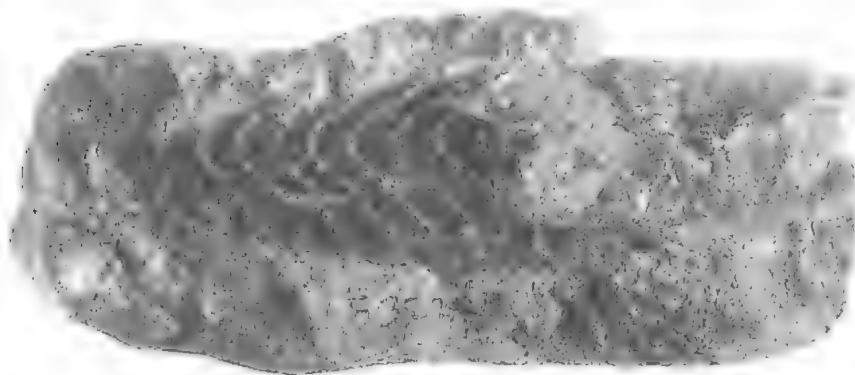


FIG. 1. QMF32208, ?orthoceratid nautiloid showing pigmentation patterns, x 1.

THE MARINE ISOPOD *NEOCIROLANA* HALE, 1925 (CRUSTACEA: CIROLANIDAE) FROM TROPICAL AUSTRALIAN WATERS

NIEL L. BRUCE

Bruce, N.L. 1994 12 01: The marine isopod *Neocirolana* Hale, 1925 (Crustacea: Cirolanidae) from tropical Australian waters. *Memoirs of the Queensland Museum* 37(1): 41-51. Brisbane. ISSN 0079-8835.

Two new species of *Neocirolana* are described from sub-littoral tropical waters of northern Australia: *Neocirolana salebra* sp. nov., from the Arafura Sea and *Neocirolana tricistata* sp. nov. from the vicinity of Torres Strait; new localities are also recorded for *Neocirolana hermitensis* (Boone, 1918) and *N. excisa* (Richardson, 1910). Observations indicate that *Neocirolana hermitensis* is a brood predator of hermit crabs. Comments are given on the current status of the genus, together with a list of all species and a key to the Indo-Pacific species. □ *Isopoda, Cirolanidae, new species, northern Australia, taxonomy.*

Niel L. Bruce, Zoologisk Museum, University of Copenhagen, Universitetsparken 15, DK 2100, København Ø, Denmark; 30 August 1994.

Neocirolana Hale, 1925 was established as a monotypic genus, later being revised by Bruce (1981, 1986). Since then Javed & Yasmeen (1990) placed a further two species in the genus, transferring *Neocirolana obtruncata* (Richardson, 1901) from *Cirolana* Leach, 1818, and describing the species *Neocirolana arabica* Javed & Yasmeen, 1990; *Neocirolana tayronae* Müller, 1993 was described from Colombia. In Australia the genus is represented by seven species, including the two new species described here, six of which occur only within the tropics.

METHODS

Methods follow those outlined in Bruce (1986, 1993).

ABBREVIATIONS

BRR- Bureau of Rural Resources; CP- circumplumose; CP- circumplumose setae; NT- Northern Territory; NTM- Northern Territory Museum, Darwin, N.T.; PMS- plumose marginal setae; Qld- Queensland, Australia; QM- Queensland Museum, Brisbane; USNM- National Museum of Natural History, Smithsonian Institution, Washington, D.C.; WA- Western Australia.

TAXONOMY

Family CIROLANIDAE Dana, 1852

Neocirolana Hale, 1925

Neocirolana Hale, 1925: 153; Holdich et al., 1981: 583; Bruce, 1981: 955, fig. 6g, h; 1986: 200; Javed & Yasmeen, 1990: 71.

TYPE SPECIES

Neocirolana obesa Hale, 1925, by monotypy.

DIAGNOSIS

Head narrow, 50 - 60% width of pereonite 1. Pleon with 5 unfused segments; posterolateral margins of pleonite 4 encompassing and extending posteriorly beyond posterior of pleonite 5. Frontal lamina ventral surface flat. Mandible incisor narrow, usually less than 50% of maximal mandible width; spine row usually with 3 - 7 spines, molar usually reduced in size (in comparison to *Cirolana*), weakly toothed. Maxillule entire, or with reduced spination. Maxilla entire or often with reduced setation and reduction in size of lobes. Pereopods robust, ambulatory, not markedly flattened or expanded; pereopods 1-3 with anterodistal angles of ischium and merus not produced or lobate. Pleopods with PMS on all rami except endopod of pleopod 5; peduncles without lateral lobes; appendix masculina basally inserted.

Additional characters. Body 2-3 times as long as wide; pereonite 1 distinctly longer than pereonite 2; posterolateral margins of pleonite 3 often extending to or beyond posterior of pleonite 5. Antennule peduncle with 3 major articles, article 4 minute; articles 1 and 2 subequal in length, partly or wholly fused. Mandible without lacinia mobilis. Maxilliped entire, or with various setal reductions, sometimes with endite reduced. Antennal peduncle 5 articulated. Mandible palp 3 articulated, extending beyond incisor. Pereopod dactylus with distinct secondary unguis. Penes short papillose or vasa deferentia

opening flush with surface of sternite 7. Uropod peduncle inner margin produced along endopod medial margin; rami provided with PMS interspersed with spines.

REMARKS

Species of *Neocirolana* all have at least some reduction of the mouthpart appendages; most species (7 of 9) have a narrow mandibular incisor, often (7 of 9) accompanied by a reduced spine row of less than 5 spines and a molar process that is smaller than that of *Cirolana*; the narrow mandible incisor appears to be associated with a narrower head width. Modifications also occur in the other mouthpart appendages, but these are mostly restricted to single species, and where similar may not be homologous. *Neocirolana excisa*, *N. maculata* and *N. obesa* all share a similar mouthpart, pereopod and uropod morphology, and appear to form a group of related species, as indicated by Bruce (1986). *Neocirolana arabica* differs from *Cirolana* only in having few (3) spines on the mandibular spine row, and could arguably be better placed in *Cirolana*. Similarly, *Neocirolana salebra*, while very similar to *Cirolana* with regard to most generic characters, differs substantially in the spination of the maxillule. In contrast, all the mouthparts of *N. obtruncata* are reduced or otherwise modified.

Two species, *N. bicrista* and *N. tricristata*, have longitudinal ridges on the pleotelson, and also have similar mouthparts, but the pereopodal morphology of the two species is distinct.

The conclusion drawn by Javed & Yasmeen (1990) that *Neocirolana* is a paraphyletic taxon for which the principal uniting character is a homoplasy is further supported by the two new species described here. The species currently placed in the genus are better retained in their present combinations, as other existing genera are less appropriate.

SPECIES OF NEOCIROLANA

Neocirolana arabica Javed & Yasmeen, 1990. Karachi coast of Pakistan, northern Indian Ocean. Types held at the QM. The species is otherwise very similar to those species of *Cirolana* which have a nodulose pleon and pleotelson, and uropods with dense setal development in the males, such as *Cirolana pleonastica* Stebbing, 1900.

Neocirolana bicrista Holdich et al., 1981. Known only from shallow subtidal depths,

Halifax Bay, Townsville, Queensland. Types held at the QM.

Neocirolana excisa (Richardson, 1910). Type locality Cabalian Point, Jolo, Philippines; common in tropical Australian waters. Syntypes held at the USNM.

Neocirolana hermitensis (Boone, 1918). An associate of hermit crabs, probably a brood predator (see species 'Remarks' given here for that species). Common in tropical Australian waters. Location of the type material is unknown.

Neocirolana maculata Bruce, 1986. Known only from the original records, Wistari Reef, Capricorn Group, southern Great Barrier Reef and Marion Reef, Australian Coral Sea. Types held at the QM.

Neocirolana obesa Hale, 1925. Type species. Types held at the Australian Museum, Sydney. Recorded distribution in southeastern Australia from Moreton Bay, southeastern Queensland to the Sydney region of New South Wales.

Neocirolana obtruncata (Richardson, 1901). Jamaica and Caribbean coast of Mexico (Martin & Felder, 1984). Types held at the USNM.

Neocirolana salebra sp. nov. Described herein.

Neocirolana tayronae Müller, 1993. Caribbean coast of Colombia, in shallow water. Holotype held at the Zoologisches Museum, Berlin.

Neocirolana tricristata sp. nov. Described herein.

KEY TO THE INDO-WEST PACIFIC NEOCIROLANA

1. Dorsal surfaces nodulose 2
Dorsal surfaces smooth, without nodules . . . 5
2. Pereon, pleon and pleotelson with distinct nodules . 3
Pereon and pleon without distinct nodules,
pleotelson with distinct longitudinal carinae . 4
3. Pereonites 7 only with nodules, pleon and pleotelson with fine nodules and pleonites 3-5 with larger paired nodules; male uropod rami lateral margin with dense mass of setae . . . *N. arabica*
Pereonites 5-7, pleon and pleotelson heavily nodulose; male uropod rami without setal mass *N. salebra* sp. nov.
4. Pleotelson with 2 widely spaced carinae and weak median carina; pereopod dactylus slender with minute secondary unguis *N. bicrista*
Pleotelson with 3 closely spaced carinae; pereopod dactylus robust with prominent secondary unguis *N. tricristata* sp. nov.
5. Uropod lateral margin without excision, apices not bifid; maxilliped endite reduced, without CPS or coupling hooks *N. hermitensis*

- Uropod lateral margin with excision, apices bifid; maxilliped endite with CPS and 2 coupling hooks 6
6. Uropod endopod deeply excised; maxilla middle and lateral lobes expanded *N. excisa*
- Uropod endopod shallowly excised, maxilla middle and lateral lobes not expanded 7
7. Cephalon anterior margin without distinct rostral point; antennular flagellum half as long as peduncle *N. obesa*
- Cephalon anterior margin with rostral point; antennular flagellum longer than peduncle *N. maculata*

***Neocirolana salebra* sp. nov.**

(Figs 1, 2)

MATERIAL EXAMINED

HOLOTYPE: ♂ (9.7 mm), Northern Territory, Arafura Sea, 11°13.5'S, 129°42'E, 12 Dec 1989, dredged 23.8m, BRR, QMW18711.

DESCRIPTION

Male holotype. Body about 2.7 times as long as greatest width; maximum width at pereonites 4-6, margins sub-parallel. Cephalon without rostral point in dorsal view; with submarginal anterior suture, with obscure ridge along medial margin of eyes; eyes large, occupying 50% width of cephalon in dorsal view; ocelli distinct. Pereonites 1-7 each with transverse suture, pereonites 4-7 becoming increasingly nodulose; coxae 2-7 not prominent in dorsal view, all with prominent entire oblique carina; posterolateral angles of coxae 5-7 acute. Pleonites all visible; pleonite 1 smooth; pleonites 2-5 nodulose, with median nodules most prominent on pleonites 3-5. Pleotelson nodulose, median nodules most prominent.

Antennule peduncle 2.8 times as long as width at article 2, articles 1 and 2 wholly fused, article 3 slightly shorter than combined lengths of articles 1 and 2; flagellum short, extending to anterior of pereonite 1, with 9 articles bearing abundant aesthetascs. Antenna peduncle articles 1 and 3 short, articles 4 and 5 subequal in length; flagellum with 14 articles, extending to posterior of pereonite 2.

Frontal lamina pentagonal, about twice as long as wide, with 2 submedian grooves. Mandible incisor with cusps indistinct, nearly as wide as maximal width; spine row with 13 spines; molar process with setules, anterior margin with 11 widely spaced spines; palp articles 2 and 3 with 13 and 14 serrate spines respectively. Maxillule lateral lobe with 11 slender spines on gnathal surface, some of which are nodulose; medial lobe with 3 very slender spines. Maxilla lateral and

middle lobe each with 3 setae; medial lobe with 2 CP spines and 9 simple setae. Maxilliped palp medial margins of articles 2-5 provided with short serrate spines, lateral margins with few setae; endite with 2 coupling hooks, 3 short simple setae and 4 long CPS.

Pereopods with few setae. Pereopod 1 merus posterior margin laterally with 6 blunt tubercular spines; 1 short acute spine, medially with 5 acute spines; posterior margin of carpus with 1 acute spine; propodus with 3 acute spines, distal spine opposing dactylus base 20% length of dactylus. Pereopod 2 posterodistal margin of ischium with 1 tubercular and 1 large blunt spine; posterior margin of merus with 3 short tubercular, 2 longer stout blunt spines, and 3 acute spines; carpus with 2 acute and 1 blunt spines at posterodistal angle; propodus palm with 3 acute spines. Pereopod 7 with anterodistal angles of ischium, merus and carpus each with cluster of large spines, some of which are serrate; posterior margins of ischium, merus and carpus with short and stout spines and cluster of spines at distal angle.

Pleopod 1 with both rami distally rounded, endopod with ~13 PMS, about 0.3 times as wide as exopod, exopod with ~40 PMS and spine at proximolateral margin. Pleopod 2 exopod and endopod with ~50 and 15 PMS respectively, appendix masculina straight with apex abruptly narrowed, extending very slightly beyond distal margin of ramus. Pleopods 3-5 exopods with the distal margin distinctly indented, with transverse suture and with about 50 PMS; endopods each with ~12, 10 and 0 PMS respectively. Uropod exopod about 0.8 times as long as endopod, straight, about 2.5 times as long as proximal width, with 2 prominent lateral submarginal nodules, lateral margin sinuate with 5 acute spines set among prominent PMS, medial margin with 4 spines among PMS, apex subequally bifid; endopod lateral margin indented at distal two-thirds of length, with prominent subapical nodule, with PMS and 1 spine adjacent to apex, medial margin smoothly convex, with 7 stout peg-like spines set among PMS; apex sub-bifid with lateral process prominent.

REMARKS

The nodulose pereon and pleon immediately distinguishes *Neocirolana salebra* from all other species in the genus. *N. arabica* has a nodulose pleon and pleotelson, but the nodules are fine except for the pairs of prominent submedial nodules on pleonites 3 and 4. There are numerous

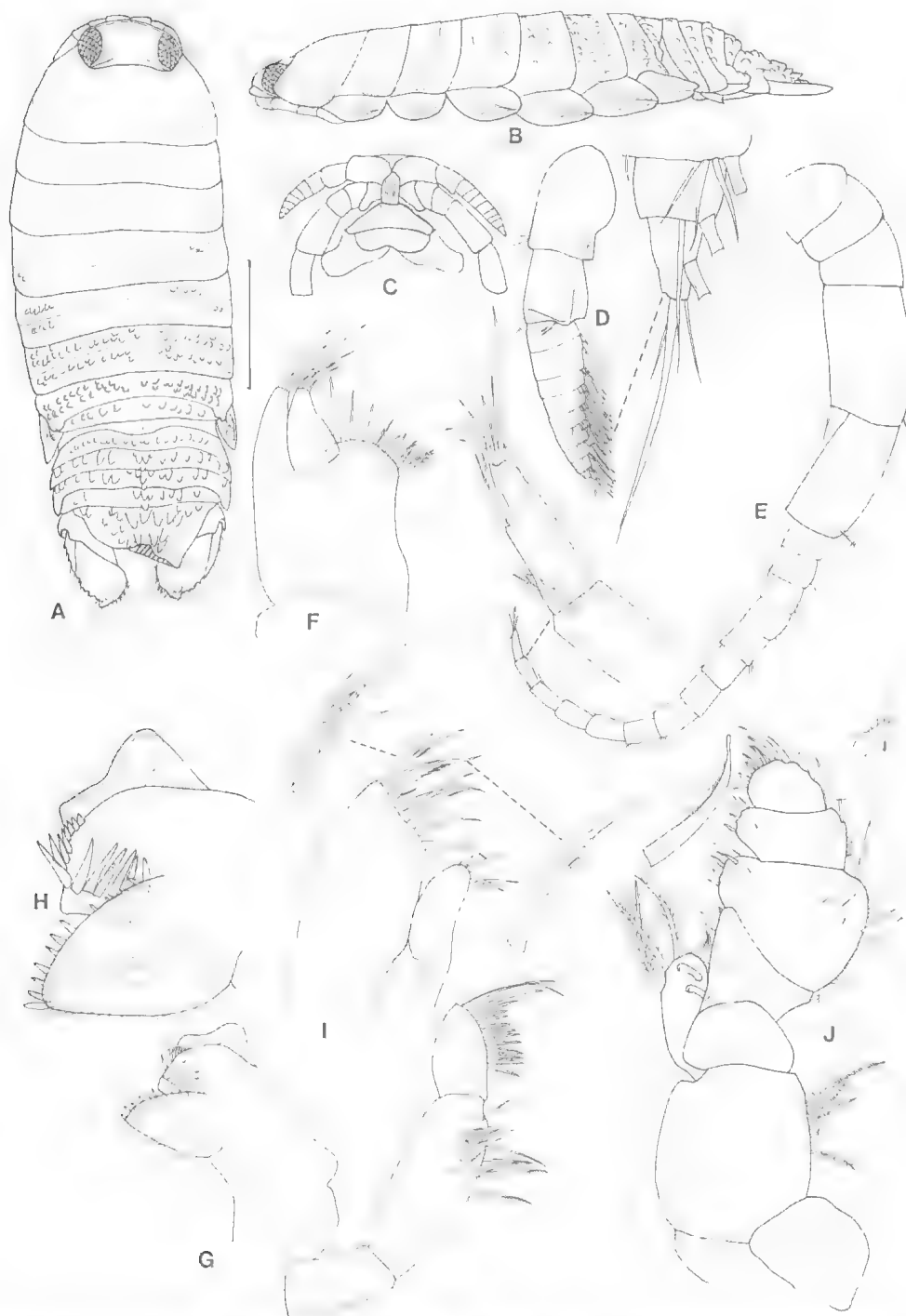


FIG. 1. *Neocirolana salebra* sp. nov. A, dorsal view; B, lateral view; C, frons; D, antennule, and detail of terminal flagellar articles; E, antenna, and detail of flagellar articles; F, maxilla; G, mandible; H, mandible, detail of incisor, molar and spine row; I, maxillule; J, maxilliped, j spine from medial margin of palp article 5. Scale = 2.0mm.

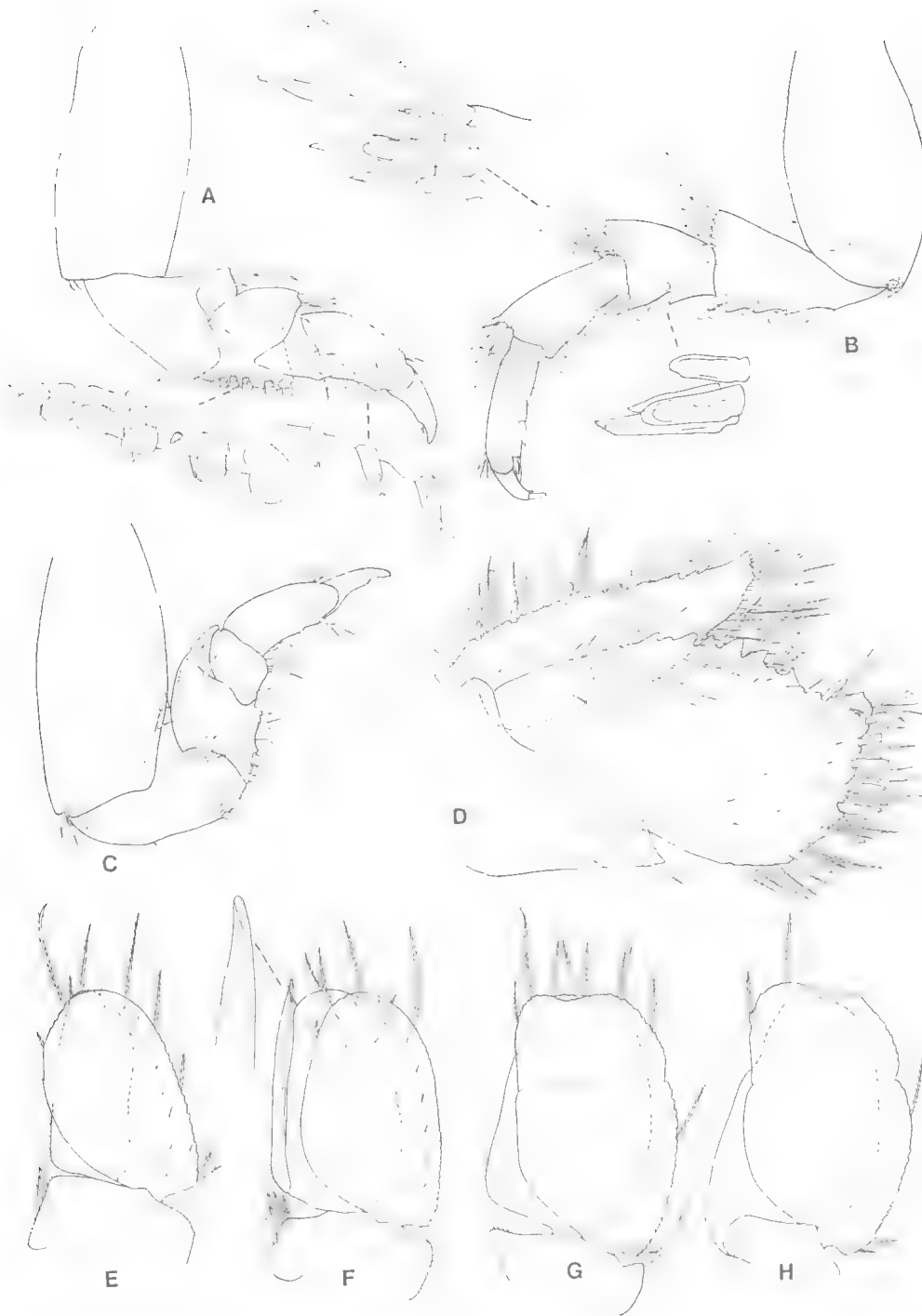


FIG. 2. *Neocirolana salebra* sp. nov. A, pereopod 1; B, pereopod 7; C, pereopod 2; D, uropod; E-H, pleopods 1-3, 5 respectively.

other differences between these two species, including the ornamentation of the frontal lamina, setation of the uropods and morphology of the mouthparts, those of *N. arabica* scarcely differing from *Cirolana*, while the mandible, maxillule and maxilliped of *N. salebra* differ significantly from that of *Cirolana*.

ETYMOLOGY

From the Latin *salebra* = rugged, uneven, alluding to the nodulose dorsal surfaces.

Neocirolana tricristata sp. nov. (Figs 3-5)

MATERIAL EXAMINED

HOLOTYPE: ♂ (3.4 mm), Gulf of Carpentaria, Queensland, 10°58.5'S, 141°12'E, 3 Dec 1990, dredged 31.0m, S. Cook on FRV *Southern Surveyor*, QMW18717.

DESCRIPTION

Male holotype. Body about 2.2 times as long as greatest width; maximum width at pereonites 3-6, margins sub-parallel. Cephalon without rostral point in dorsal view; anterior margin thickened, with submarginal anterior suture, with obscure longitudinal ridge along medial margin of eyes; eyes occupying 44% width of cephalon in dorsal view; ocelli distinct. Pereonites 1-7 each with transverse suture, becoming laterally more prominent on pereonites 5-7; coxae 2-5 not prominent in dorsal view, all coxae with prominent entire oblique carina; postemlateral angles of coxae 5-7 acute. Pleonites all visible, pleonites 2-5 with finely nodulose posterior margin. Pleotelson with submarginal nodule at anterolateral angle; lateral margins obscurely thickened; dorsal surface with 3 distinct longitudinal ridges consisting of median ridge flanked by further ridge on either side; posterior margin evenly rounded, with 4 spines set among PMS.

Antennule peduncle robust, 2.5 times as long as width at article 2, articles 1 and 2 partially fused, article 3 about half as long as the combined lengths of articles 1 and 2; flagellum short, extending to anterior of pereonite 2, with 9 articles bearing conspicuous spray of aesthetascs. Antenna peduncle dorsoventrally compressed, article 1-3 short, articles 4 longest, 1.4 times longer than article 5; flagellum with about 9 articles, extending to posterior of pereonite 2.

Frontal lamina pentagonal, about twice as long as wide, lateral margins weakly concave, with 2 submedian grooves. Mandible incisor narrow,

about 50% maximal width, with distinct cusps; spine row with several setae and 3 spines; molar process short, with few setules, anterior margin with about 7 widely spaced spines; palp articles 2 and 3 with about 10 and 7 serrate spines respectively. Maxillule lateral lobe with 12 slender spines on gnathal surface, several of which serrate; medial lobe with 2 CP spines. Maxilla lateral and middle lobe with 3 and 4 setae respectively; medial lobe with 5 CP spines and 3 simple setae. Maxilliped palp articles lateral margins with few setae; endite with 1 coupling hooks, 3 short CPS.

Pereopods robust, with few setae. Pereopod 1 merus posterior margin with 3 blunt tubercular spines and 1 acute spine; posterior margin of carpus with 1 acute spine; propodus with 1 acute spine, and distal spine opposing dactylus base 38% length of dactylus. Pereopod 2 posterodistal margin of ischium with 1 tubercular spine; posterior margin of merus with 3 tubercular and 2 long acute spines; carpus with 2 acute spines at posterodistal angle; propodus palm with 1 acute spine. Pereopod 7 with anterodistal angles of ischium, merus and carpus each with cluster of large spines, some of which are serrate; posterior margins with short simple acute spines at distal angles, ischium with 3 short acute spines along posterior margin, merus, carpus and propodus with 1 each.

Pleopod 1 with both rami distally rounded, endopod about 3 times as long as wide, about 0.5 as wide as exopod; exopod with ~20 PMS and spine at proximolateral margin, endopod with ~10 PMS. Pleopod 2 exopod and endopod with ~26 and 9 PMS respectively, appendix masculina distally curving slightly towards lateral margin, apex extending beyond distal margin of ramus by half of its length. Pleopods 3-5 with similar, exopods each with the distal margin rounded, each with transverse suture and with about 25 PMS; endopods each with ~10, 6 and 0 PMS respectively. Uropod exopod about 0.9 times as long as endopod, straight, about 3 times as long as proximal width, lateral margin straight, irregularly notched with 4 short spines, each set in notch, and 7 PMS, medial margin with 2 spines among PMS, apex subequally bifid with cluster of setae and small spine within apical notch; endopod lateral margin indented with 4 PMS and 1 spine adjacent to apex, medial margin serrate, smoothly convex, with 3 stout peg-like spines set among PMS; apex subequally bifid with cluster of setae and two small spines within apical notch.

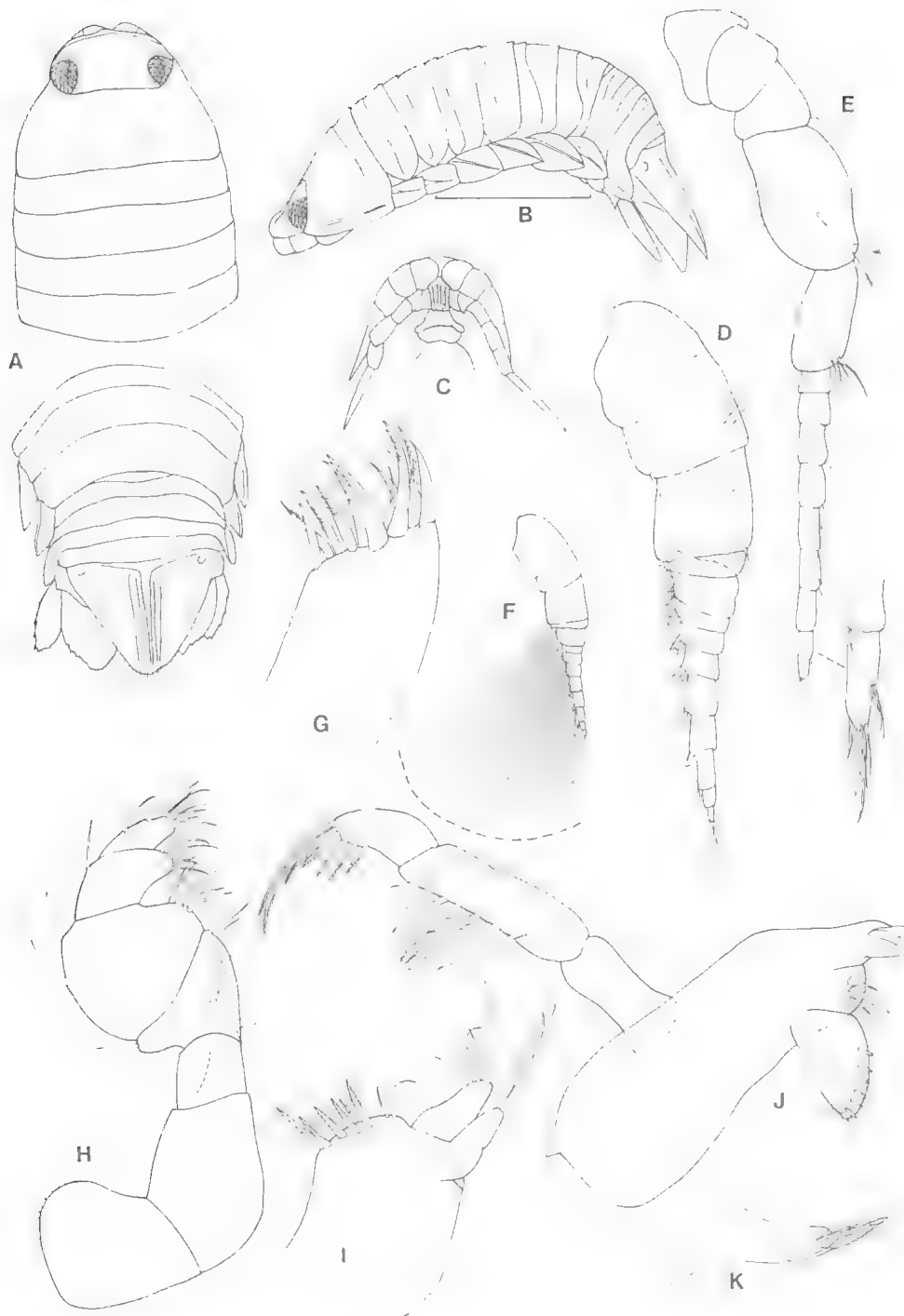


FIG. 3. *Neocirolana tricristata* sp. nov. A, dorsal view; B lateral view; C, frons; D, antennule; E, antenna; F, antennule, showing spread of aesthetascs; G, maxillule, lateral lobe; H, maxilliped; I, maxilla; J, mandible; K, maxillule, medial lobe in oblique view. Scale = 1.0mm.

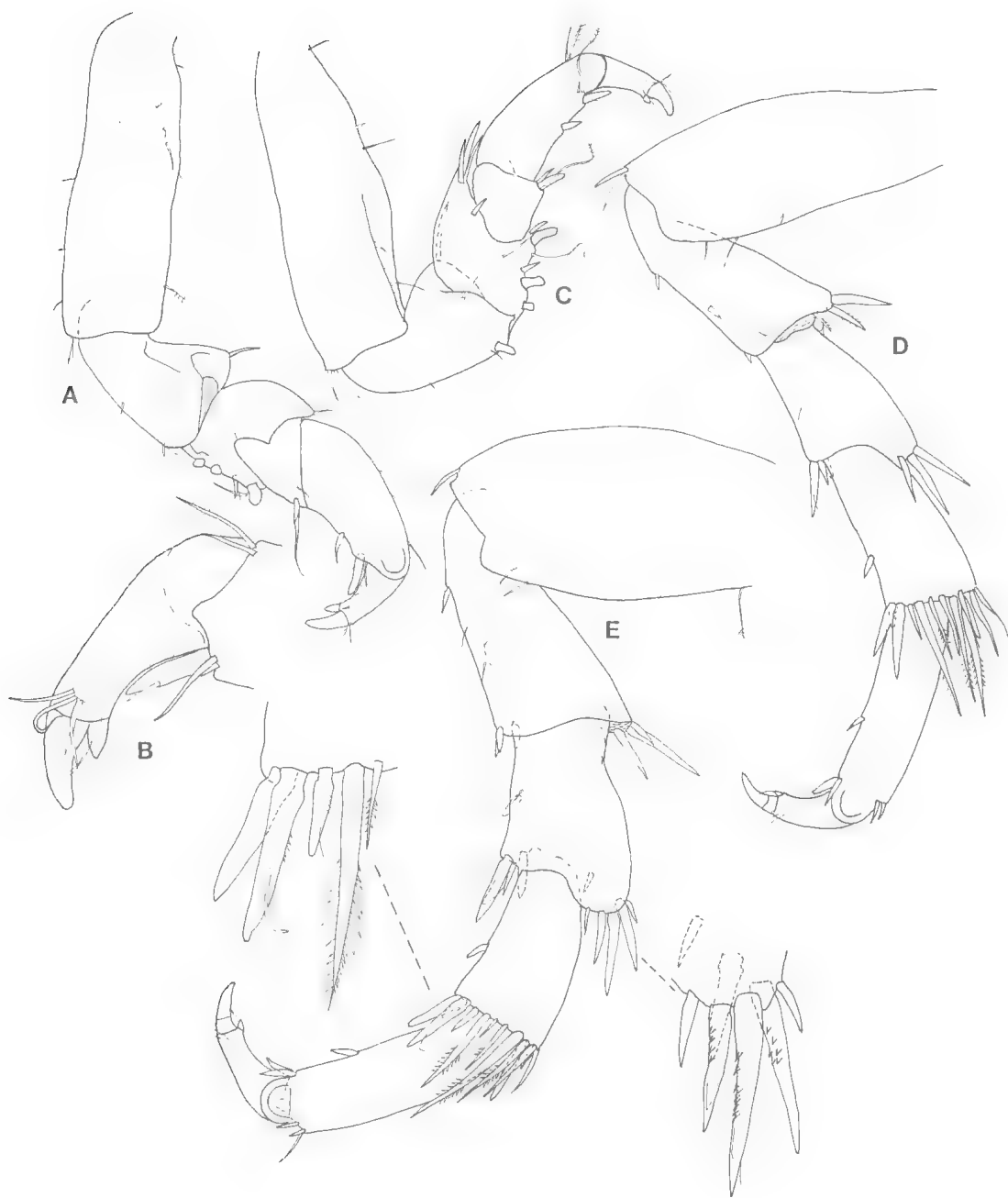


FIG. 4. *Neocirolana tricristata* sp. nov. A, pereopod 1; B, pereopod 1, dactylus, medial view; C, pereopod 2; D, pereopod 6; E, pereopod 7.

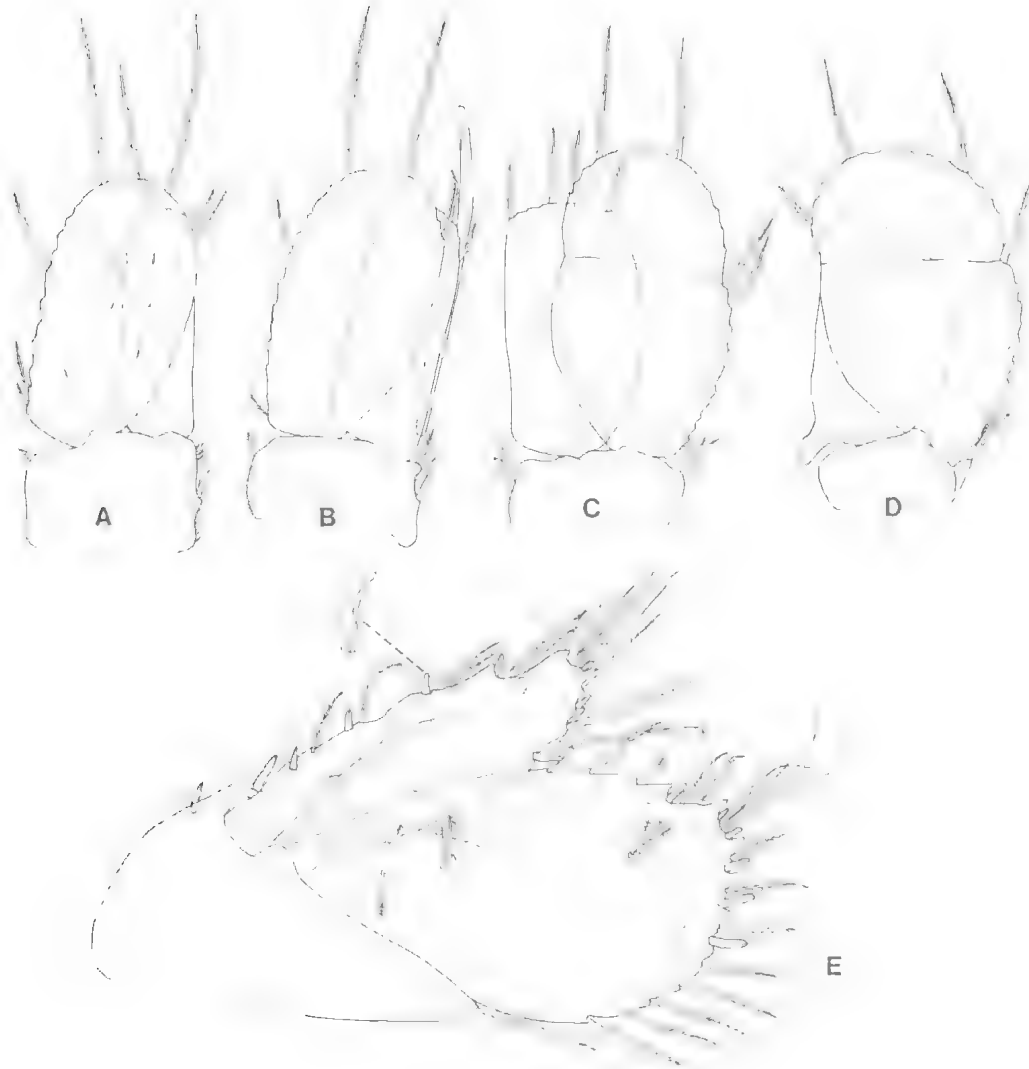


FIG. 5. *Neocirolana tricristata* sp. nov. A-D, pleopods 1-3, 5 respectively; E, uropod.

REMARKS

This species is readily separated from others of the genus by the three prominent pleotelsonic ridges and the antennular morphology. *Neocirolana bicrista* has two ridges on the pleotelson and a third weakly defined median ridge. *N. tricristata* has a maxilla and maxilliped that are similar to that of *Cirolana*, the maxilliped having the mediodistal angles of palp articles 2 - 4 somewhat produced and lobate, and provided with abundant slender

setae. In contrast, in *N. bicrista* the maxilla has no large circumplumose setae on the medial lobe and has prominent recurved setae on the middle and lateral lobes; the maxilliped has cuticular setules along both margins of the palp, but few setae, and the mediodistal angles are scarcely produced and have only 1 or 2 short setae. The pereopods of *N. tricristata* differ from that of *N. bicrista* being more robust and in having a prominent spine opposing the dactylus base and a prominent secondary un-

guis to the dactylus, both of these being minute in *N. bicrista*.

The antennule flagellum has a dense mass of aesthetascs, and is similar in form to a calynophore (Lowry, 1986). The definition of a calynophore includes the total or partial fusion of the proximal articles (Lowry, 1986), and as the articles of *N. tricristata* are unmodified in that way, nor are they particularly enlarged, the aesthetasc mass is not regarded as a calynophore.

ETYMOLOGY

From the Latin *crista* = ridge, alluding to the three pleotelsonic ridges.

Neocirolana excisa (Richardson, 1910)

Cirolana excisa Richardson, 1910: 6, figs 4, 5; Nierstrasz, 1931: 156; Bruce, 1980: 127, 128.

Neocirolana excisa: Bruce, 1981: 957; 1986: 207, figs 144, 145; Javed & Yasmeen, 1990: 72, table 1.

MATERIAL EXAMINED

ARAFURA SEA: ♀, non-ovig, 10°32.6'S, 134°16.6'E, 13 Oct 1992, 60m, R.W. Williams, NTMCR009778; ♂, 11°18.3'S, 129°24.0'E, 21 Nov 1989, 34.7m, BRR, QMW18710; ♀, 11°00.0'S, 132°47.0'E, 30 Oct 1989, 18.3m, BRR, QMW18712. NORTHERN TERRITORY: ♂, Channel Is, Darwin, 20 Aug 1982, ex sponge 'A', 11m, P. Horner, NTMCR005822; 3 ♀, 2 ovig, 1 non-ovig, Coral Bay, Port Essington, Coburg Peninsula, 11 Aug 1986, ex sponge, R. Williams, NTMCR004142; ♀, non-ovig, north of Wessel Island, 16°32.5'S, 121°24.5'E, 17 Apr 1983, 40m, W. Houston, NTMCR002976. GULF OF CARPENTARIA: 2 ♂, far northern Gulf, Qld, 10°04.1'S, 141°24.4'E, 1 Apr 1989, dredged, 61.0m, BRR, QMW19715.

REMARKS

Previously known from two records only, the species is not uncommon along Australia's northern coasts from the intertidal to a depth of 61m; two records are from sponges. It has not been taken from coral reef habitats and may inhabit only inshore and offshore habitats with a high silt load.

DISTRIBUTION

Originally recorded (Richardson, 1910) from the Philippines, the species is now recorded from Australia's tropical northern waters from the Arafura Sea to Torres Strait at depths from 11 to 61m. It has not been collected from tropical eastern Queensland, despite collecting ef-

forts in that region, and its range may not extend to that area.

Neocirolana hermitensis (Boone, 1918)

Cirolana hermitensis Boone, 1918: 592, pl. 31, fig. 2; Hale, 1925: 132.

Neocirolana hermitensis: Bruce, 1981: 956; 1986: 202, figs 140, 141; Javed & Yasmeen, 1990: 72, table 1.

MATERIAL EXAMINED

TIMOR SEA: ♂, Oxley Island, 10°59.0'S, 132°48.8'E, 19 Oct 1982, low water spring level, ex *Dardanus* sp. A.J. Bruce, NTMCR002282; ♀, ovig, Hibernia Reef, 11°59'S, 123°22'E, 15 May 1992, 0-0.5m, on reef flat in *Turbo* shell with *Calcinus gaimardii*, J. Short, QMW14232; 3 ♂, 2 ♀, ovig, 'Ann Millicent' wreck, Cartier Reef, WA, 12°32.8'S, 123°32.9'E, 4 May 1992, intertidal, in *Bursa granularis* shell, R. Williams & B. Russel, NTMCR009613; ♂, ♀, non-ovig, North West Island, Ashmore Reef, 21 Sept 1987, intertidal, ex *Dardanus*, H. Larson, NTMCR005981. TORRES STRAIT: Juvenile, 10°02'S, 142°31'E, 21 Apr 1974, 13m, Qld Fisheries Service, QMW17960; ♂, ♀, 9°56.2'S, 141°55.5'E, 3 Apr 1989, 39m, dredged, BRR, QMW18714; ♂, 10°22.4'S, 141°30.3'E, 4 May 1989, 65m, dredged, BRR, QMW18716.

REMARKS

This species is regularly recorded from gastropod shells that are, or have recently been occupied by hermit crabs prior to collection, usually by species of *Dardanus*. Recently a specimen was collected by J.D. Shields at Bird Islet, Lizard Island in association with a female *Dardanus scutellatus*. The isopod left when the shell was cracked open to remove the crab, and immediately swam to the ovigerous host and was seen to be eating the eggs. The remains of eggs were also observed in its gut. It seems very probable, therefore, that *Neocirolana hermitensis* is an egg predator, a habit which has been recorded only for one species of deep-water lysianassoid amphipod (Bowman & Wasmer, 1984), but not previously for the Cirolanidae, nor any other marine isopod.

DISTRIBUTION

Most records are from offshore coral reef habitats around the Australian coast, with the exception of one record from inshore coral reefs at Port Essington, NT (Bruce, 1986); from the Montebello Islands, WA, to Lizard Island, Qld, Australia.

ACKNOWLEDGEMENTS

I am indebted to Dr Jeffrey D. Shields (Virginia Institute of Marine Science, The College of William & Mary, Virginia, U.S.A.) for providing the information on his observations of the dietary habits of *Neocirolana hermitensis*. I also thank Stephen Cook (QM) for delivery of specimens from the Gulf of Carpentaria, and P.J.F. Davie (QM) and A.J. Bruce (NTM) for the opportunity to examine material under their care. I thank Jørgen Olesen for his inking of the figures.

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MALE COMBAT IN THE BLACK WHIP SNAKE, *DEMANSIA VESTIGIATA*. *Memoirs of the Queensland Museum* 37(1): 52, 1994. Male combat is well known in Australian elapids and boids (Shine, 1991). It has been reported in many elapid genera - *Austrelaps*, *Cryptophis* (now *Rhinoplocephalus*), *Demansia*, *Hemiaspis*, *Notechis*, *Oxyuronus*, *Pseudechis* and *Pseudonaja*. These genera are characterised by male size superiority. Male combat is unknown in genera in which females are larger than males e.g. *Acanthophis* and *Vermicella*, (Shine & Allen, 1980; Shine, 1991). Shine (1978) first reported this sexual dimorphism/male combat correlation and has commented on its adaptive significance (Shine, 1981, 1991). He summarised this as a '... male strategy for (i) forcing rival males to flee from the vicinity of a receptive female ... (ii) physically "carrying" rival males away from a female ... (iii) defending against homosexual courtship ... and (iv) gaining access to food ...' (Shine, 1981).

We report recent observations of male combat in *Demansia vestigiata* and present photographs of combat in this species. On June 13, 1994 two snakes were encountered 11 km south of the Starcke R., NEQ (14°51'S, 145°02'E), in a grassy open forest dominated by *Melaleuca viridifolia*. (This is typical habitat for *D. vestigiata* on Cape York Peninsula). At about 4.00pm they were found in the open, in the wheel rut of the unsealed track from Cooktown to the Starcke R. They were observed and photographed (Fig. 1 A-C), but were not examined to check sex. However, as mating has been observed by one of us (JC) to be relatively passive in this species; as the snakes were observed very closely (from a distance of about 5m) and were not copulating; as they were large (with TLs of approximately 70cm); and their behaviour was very similar to that reported for male combat in other elapid species, we are confident both snakes were males. We watched their ritual for close to 45 minutes. They moved, as a pair, about 20m along the road - all the time twisting, coiling, raising their forebodies both together and separately, and then falling back to begin the sequence anew.

Male combat in *D. vestigiata* has been recorded before, briefly. Shine (1980) noted an observation by Neil Charles, near Cooktown, 22 September (year not cited). '... The two males were plaited together in typical ritualised combat ... were captured and their sex confirmed ...'. It has also been photographed before by J. Stanicic, D. Potter and J. Chaseling, 21 September, 1988, near the Captain Billy Landing turn-off, Cape York Peninsula. Their photographs have been lodged in the Queensland Museum Photographic Index (NP119-21). *Demansia vestigiata* is a species in which the males exceed females in size. Our observations conform with several strategies suggested by Shine (1981) to explain this behaviour. The activity carried both snakes far from their starting point in the short period they were observed closely. Shine (1980) observed '... no clear seasonal pattern (in reproduction) is evident in *D. atra* (now *D. vestigiata*) ...'. Our Winter observation, considered with the only others known (in Spring) is consistent with this.

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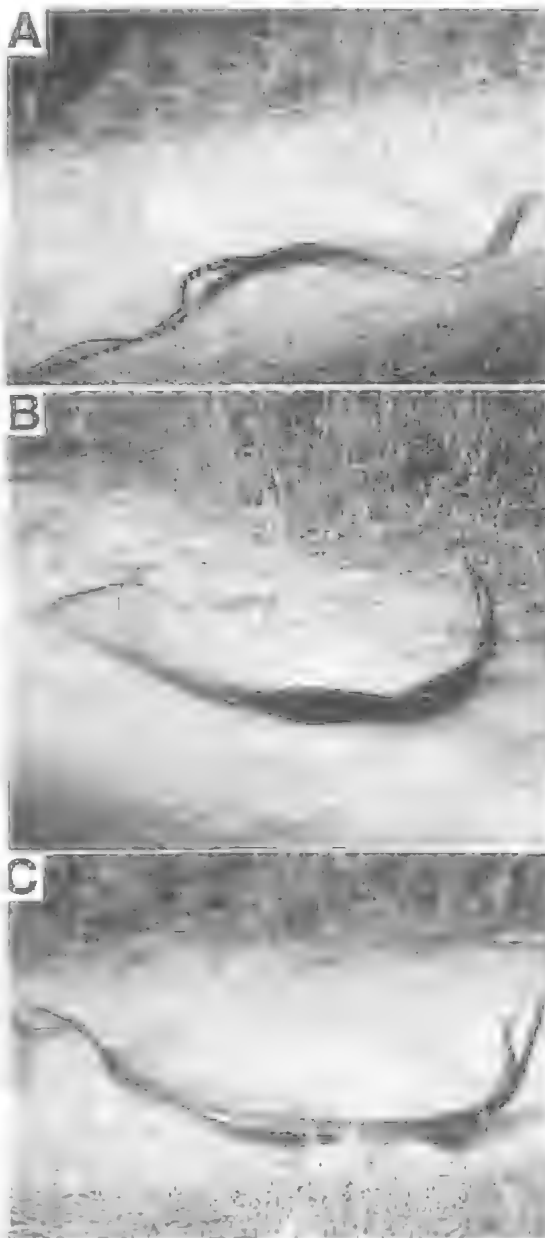


FIG. 1. A-C, *Demansia vestigiata*, males in combat, Starcke R., NEQ.

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 J.A. Covacevich, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; L. Roberis, Shipton's Flat, via Cooktown, Queensland 4871, Australia; I. McKinna, James Cook Museum, Cooktown, Queensland 4871, Australia; 10 August 1994.

REDESCRIPTION OF *NEPHRURUS ASPER* GÜNTHER, AND DESCRIPTION OF
N. AMYAE SP. NOV. AND *N. SHEAI* SP. NOV.

PATRICK J. COUPER AND ROBERT A.M. GREGSON

Couper, P.J. & Gregson R.A.M. 1994 12 01: Redescription of *Nephrurus asper* Günther, and description of *N. amylae* sp. nov. and *N. sheai* sp. nov. *Memoirs of the Queensland Museum* 37(1):67-81. Brisbane. ISSN 0079-8835.

Three allopatric species, clearly defined by morphology and colour pattern, comprise the *N. asper* species complex. *N. asper* is confined to Queensland (10°53'S-25°21'S), and has a distinctive, boldly banded colour morph occurring on Cape York Peninsula (extending south to Mt Surprise, 18°21'S); *N. amylae* sp. nov. to the south-central Northern Territory and *N. sheai* sp. nov. to the Kimberley region of Western Australia and the Arnhem Escarpment of the Northern Territory. All three species occur in open woodland habitats where they feed on a wide range of arthropod species. Males are in reproductive condition during the summer months and gravid females are present in the population from mid-summer to autumn for *N. asper* and *N. amylae*. *N. sheai* may be sexually active throughout the year. □ *Gekkonidae*, *Nephrurus*, *systematics*, *new species*, *distribution*, *open woodland*, *diet*, *reproduction*.

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Nephrurus asper was described from a single specimen (BMNH1946.8.23.34) from Peak Downs Stn, mideastern Queensland (22°56'S, 148°05'E). Subsequently, specimens matching the type description have been recorded from most of northern Australia (Cogger, 1992).

While the distinctive morphology of *N. asper* has ensured its nomenclatural stability (Cogger et al., 1983), several authors have commented on geographical variation within the species. Storr (1963) noted differences in tail length between specimens from Western Australia and Queensland. Bauer (1990) observed that specimens from the south-central Northern Territory were larger than those in other parts of the range. Wilson and Knowles (1988) recognised the broad-banded form of *N. asper* from Cape York Peninsula as distinct from other populations of this species.

An examination of all *N. asper* held in the collections of major Australian museums revealed that the species, as currently recognised, could be divided into four geographically distinct groups (Arnhem Escarpment, NT & Kimberley region, WA; south-central NT; Queensland & Cape York Peninsula) on the basis of colour, pattern, spinosity, and other scale characters. Pattern and spinosity have been used widely in gekkonid revisionary work (Couper et al., 1993; Storr, 1988, 1989). They have been found to be useful in delineating the species in the *N. asper* complex, in a way which conforms closely with statistical analyses.

The current study is augmented by Kolmogorov Smirnov Two-sample Tests and multivariate discriminant analyses. These analyses, performed using body measurements and quantitative scale counts only, provide an independent assessment of the morphological identity of the four geographic groups identified on colour pattern and/or degree of spinosity.

The statistical analyses were conducted by one of us (RAMG) and the taxonomic analysis was conducted by the other (PJC)

All measurements were taken using Mitutoyo electronic callipers. Abbreviations for body measurements are as follows: snout-vent length (SVL); axilla to groin (AG); tail, tip to constriction at base (T); tail, tip to vent (TV); knob width (KW); forelimb, axilla to tip of longest digit (L1); hindlimb, groin to tip of longest digit (L2); neck length, axilla to posterior edge of ear (NL); head length, tip of snout to dorsal/anterior margin of ear (HL); head width, measured between ear openings (HW); head depth, from above eyes to ventral margin of maxillae (HD); snout, tip to anterior margin of orbit (S); eye to ear, posterior margin of orbit to anterior margin of ear (EE). Abbreviations for scale counts and caudal annuli are as follows: number of granular scales in direct contact with dorsal edge of rostral scale (R); number of interorbital scales counted across the narrow, bony bridge between the orbits, includes the enlarged series of scales on either side (I); number of supralabial scales counted to exclude granular scales towards angle of mouth (SL);

TABLE 1. Differentiation between groups using a KS2 Procedure χ^2 from the 6 possible comparisons between the 4 samples. N is the number of contrasts with KS2d χ^2 statistic > 6. The .05 level for χ^2 is about 5.99, for the .01 level is about 9.21, for the .001 level is about 13.81.

| body character | GROUPS | | | | | |
|----------------|--------|--------|--------|--------|--------|--------|
| | 1 vs 2 | 1 vs 3 | 1 vs 4 | 2 vs 3 | 2 vs 4 | 3 vs 4 |
| T | 6.59 | 3.69 | 4.94 | 4.00 | 0.47 | 3.88 |
| TV | 18.00 | 5.81 | 3.24 | 5.83 | 0.52 | 2.31 |
| KW | 6.50 | 7.53 | 0.24 | 22.99 | 3.88 | 1.61 |
| TA | 9.44 | 4.30 | 4.10 | 0.35 | 0.59 | 0.44 |
| L1 | 1.35 | 4.34 | 1.80 | 1.05 | 0.92 | 0.44 |
| L2 | 0.52 | 3.98 | 1.81 | 2.07 | 0.48 | 2.57 |
| HW | 0.70 | 8.03 | 1.33 | 7.16 | 0.41 | 5.63 |
| HL | 0.26 | 7.19 | 0.59 | 4.88 | 1.11 | 1.44 |
| S | 1.31 | 7.11 | 2.14 | 9.20 | 3.71 | 5.87 |
| NL | 6.32 | 6.17 | 1.58 | 15.64 | 1.44 | 3.07 |
| SL | 25.32 | 24.93 | 17.59 | 1.24 | 2.55 | 3.44 |
| IL | 35.80 | 26.48 | 15.38 | 0.73 | 2.41 | 1.32 |
| R | 3.40 | 30.75 | 0.79 | 30.13 | 3.79 | 9.45 |
| I | 19.84 | 35.28 | 6.04 | 7.42 | 0.20 | 2.84 |
| EE | 2.97 | 0.92 | 7.50 | 4.19 | 2.85 | 7.32 |
| HD | 0.09 | 5.43 | 1.98 | 4.60 | 2.10 | 7.78 |
| AG | 0.32 | 2.35 | 1.65 | 1.37 | 1.11 | 0.26 |
| N | 8 | 9 | 4 | 6 | - | 3 |

number of infralabial scales counted to exclude granular scales towards angle of mouth (IL), and number of caudal annuli counted between basal constriction and distal knob (TA).

OTHER ABBREVIATIONS USED: Queensland Museum (QM), Australian Museum (AM), Museum of Victoria (NMV), South Australian Museum (SAM), Western Australian Museum (WAM) and the Northern Territory Museum (NTM), Cape York Peninsula (CYP), mideastern Queensland (MEQ), Queensland (QLD), Northern Territory (NT), Western Australia (WA).

Reproductive and dietary data were compiled by examination of specimens in which the body cavity had already been opened.

STATISTICAL ANALYSES

The following data analyses have been performed, using complete records on 149 animals. Some are internal checks on consistency and are hence not reported in full here. The characters used in these analyses are the body measurements and scale counts defined above. Group 1 = the

Arnhem Escarpment (NT) & Kimberley region (WA), group 2 = QLD, group 3 = south-central NT, and group 4 = CYP.

1. The Kolmogorov Smirnov Two-sample Test (KS2) (Kolmogorov, 1941; Smirnov, 1939) on each of the 6 pairwise contrasts between groups on each of 17 characteristics, giving a total of 10 χ^2 values each with 2 d.f. This is a nonparametric procedure, using minimal prior assumptions about the form of frequency distributions of measurable characteristics (Walsh, 1965).

It indicates which characteristics differentiate better than at some given probability level, if the characteristics are independent. This is not strictly true a priori, and hence conservative probability levels may be used in deciding what results to accept. It also will fail to detect second-order measures, such as ratios or differences of characteristics, which can be non-linear and of use, unless these are built into the data. The measures in mm have been divided by SVL, those based on scale counts have not. Bilateral measures have been pooled (Table 1). Discriminant analyses have also been run because they can utilise linear (but only linear) combinations of characteristics, and hence may separate groups which are not distinguished on single characteristics (Table 1). The discriminant analyses do, however, make some distributional assumptions approximating to normality and homoscedascity across groups.

The role of the KS2 is also involved with the question of what characteristics to use in the discriminant analysis, if not all the characteristics which have been measured are used.

2. The correlation matrix on the characteristics over the whole 149 complete records used. This showed that the rank of the data is much less than 17; this indicated, as expected, that there is redundancy in the morphological data.

3. Four discriminant function analyses (Rao, 1952):

3.1. Using all the characteristics, on raw measures.

3.2. Using a stepwise discriminant analysis, on raw measures.

3.3. Using all the characteristics, on measures divided by SVL.

3.4. Using a stepwise discriminant analysis, on measures divided by SVL.

The stepwise procedures are inbuilt to the SPSSx program used; because of the intercorrelations noted under part (2) above, the variables retained in a stepwise analysis will depend on those intercorrelations and on the relative sizes of the four groups, but will be analogous to the

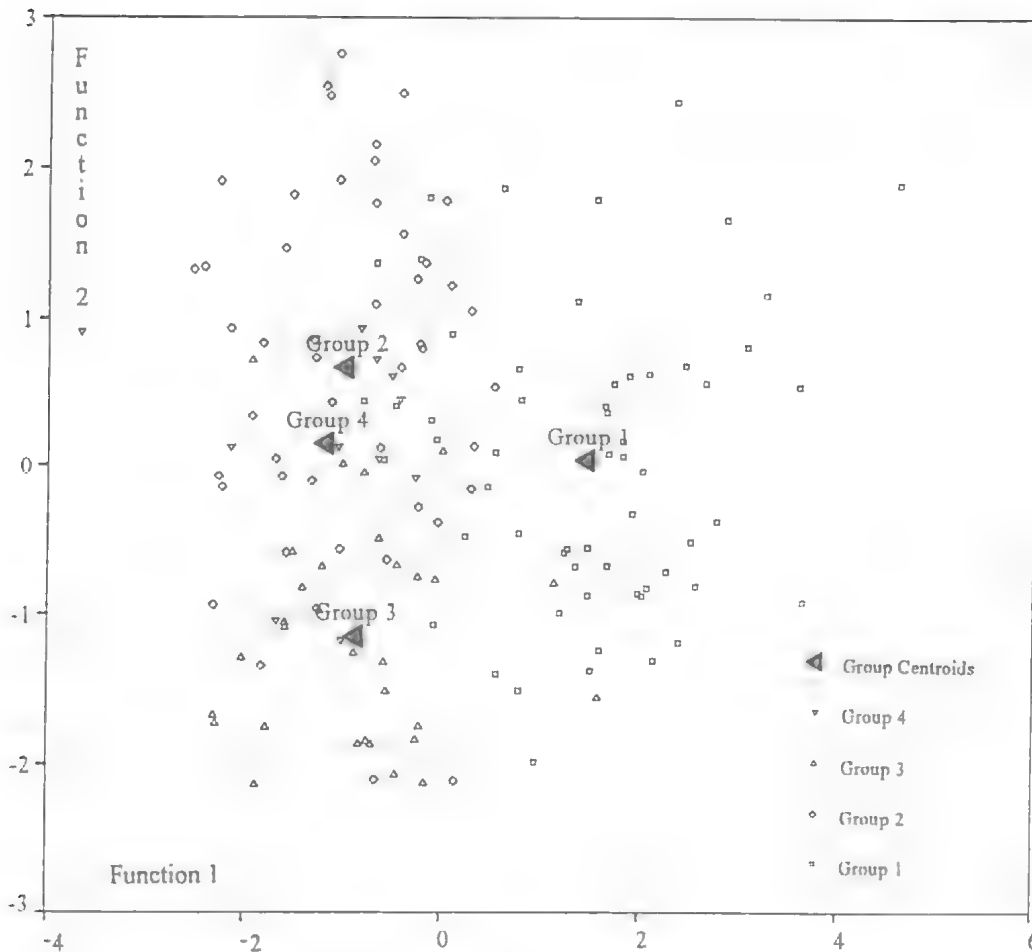


FIG. 1. Plot of the individuals and group centroids on the 1st two canonical variates from the discriminant analysis. Group 1 = the Arnhem Escarpment (NT) & Kimberley region (WA), group 2 = QLD, group 3 = south-central NT, and group 4 = CYP.

characteristics with larger χ^2 values in Table 1. We present tables derived from (3.4) here; as there are only 11 animals in the smallest group, the number of variables in the discriminant analysis has to be reduced to below 10. The stepwise procedure is the most appropriate for this, retaining only those variables with discriminative power; it showed by F-tests that only eight variables were legitimately retained in the analysis.

Information for the identification of new specimens when allocation is based on body measurements and scale counts only is not in itself sufficient (Tables 2, 3). Allocation to species must also take into consideration colour pattern and degree of spinosity. The relative values of the coefficients (Table 3) are of use,

they are weights to multiply with corresponding measurements, and then sum the products and add the constant term in the column. As additional specimens become available it is preferable to incorporate them in an extended discriminant analysis, thus yielding new weights. The efficiency of allocation decisions using this discriminant analysis is summarised (Table 4); it will be noted that the relatively poor separation of group 2 (QLD) and group 4 (CYP) is compatible with the results from the KS2 analysis.

RESULTS

The plot of individuals and group centroids on the first two canonical variates from the discriminant analyses (Fig. 1) gives a picture com-

TABLE 2. Standardised discriminant function coefficients and correlations with discriminant functions from the stepwise analysis with three canonical functions. Ic = coefficients for the first discriminant, Ir = its correlations with discriminating variables, and so on.

| char | Ic | Ir | IIc | IIr | IIIc | IIIr |
|------|--------|-------|-------|------|--------|-------|
| HW | .070 | .112 | .511 | .475 | -.706 | -.415 |
| I | 1.453 | .388 | -.209 | .470 | -1.234 | -.201 |
| LI | .392 | .187 | -.459 | .102 | -.472 | .107 |
| NL | -.161 | -.118 | .398 | .432 | -.207 | .191 |
| R | -.114 | .204 | 1.147 | .737 | 1.023 | .159 |
| SL | .864 | .360 | -.367 | .358 | 1.121 | .122 |
| TA | -1.750 | .081 | .122 | .431 | -.956 | .086 |
| TV | -.577 | -.327 | -.138 | .271 | .124 | -.122 |

patible with Tables one and four. Group 2 (QLD) and group 4 (CYP) are not significantly separable on external morphology. The recognition of group 4 was based on colour-pattern. The uniformity in morphology between groups 2 and 4 dovetails well with preliminary genetic data which show a low level of divergence between a broad-banded specimen from Heathlands, CYP and a specimen from the Capella region of MEQ (Couper & Donnellan, unpubl. data). All QLD material examined in this study, with the exception of the broad-banded specimens from CYP, is consistent with the holotype of *N. asper* (BMNH1946.8.23.34) in both colour-pattern and scalation (see Remarks for *N. asper*) and is here assigned to this taxon. The broad-banded CYP specimens are regarded as a geographically distinct colour morph of *N. asper*. The statistical analyses show that group 1 (Arnhem Escarpment, NT & Kimberley region, WA) and group 3 (south-central NT) are morphologically distinguishable from QLD and CYP combined as a single group (Table 1, Fig. 1) and also from each other. Groups 1 and 3 are here described as new, allopatric taxa. The recognition of these taxa is further supported by preliminary genetic data (Couper & Donnellan, unpubl. data).

The 'Atlas of Australian Resources' (Anon. 1952-69) shows reasonable conformity between the distribution of the *N. asper* species complex and the occurrence of upland country and heavy, often stony soils. However, the zoogeographical implications of this distribution can not be assessed without first establishing a phylogeny for the genus and determining the dates of speciation events. Presently, there is no fossil record for *Nephrurus* and biochemical studies are incomplete.

SYSTEMATICS

Nephrurus asper Günther, 1986 (Fig. 2A,B; Statistical analyses groups 2, 4)

MATERIAL EXAMINED

QUEENSLAND: QMJ22179, QMJ24921, Bamaga, Cape York Peninsula (10°53'S 142°24'E); QMJ57652, 6.5km E of Heathlands airstrip (11°44.33'S 142°38.28'E); QMJ54644, Heathlands road, 1km from main Cape road junction (11°46'S 142°40'E); QMJ40165, Weipa to Aurukun, mid-way, N Camp Beagle Airstrip (13°05'S 141°57'E); QMJ738, Kingsborough (16°55'S 145°02'E); QMJ4960, Bullock Ck, via Cairns (16°55'S 145°46'E); QMJ57993, QMJ58850, Elizabeth Ck, nr Bulleringa NP, N of Mt Surprise (18°00'21"S 145°59'50"E); QMJ2125, ? Northern Rivers; QMJ44689, New Moon Stn (19°12'S 145°44'E); QMJ3443, Charters Towers, Black Jack (20°08'S, 146°13'E); QMJ42015, Hughenden, approx 2km W of Iona-Redcliffe Stn Homestead (20°59'S 144°33'E); QMJ44948, Egera Stn (20°59'S 146°05'E); J143, Natal Downs (21°05'S, 146°09'E); QMJ4525-6, Kuridala, S of Cloncurry (21°17'S 140°30'E); QMJ15565, 80km SW of Mackay (21°39'S 148°42'E); QMJ31976, QMJ35040, Winton (22°23'S 143°02'E); QMJ5727, Lucknow Stn, W of Winton (22°43'S 140°55'E); QMJ1355, QMJ3552, Clermont (22°50'S 147°38'E); QMJ28699, Cork Stn via Winton (22°56'S 142°18'E); QMJ46720, Aramac Range, Winhaven Stn (22°57'S 145°41'E); QMJ56088, Capella, 20km N on Clermont road (22°59'S 147°53'E); QMJ36795, Moongoo (23°10'S 148°04'E); QMJ3767, Rockhampton, Dalma, Waroula (23°20'S 150°32'E); QMJ9912, Longreach (23°26'S 144°15'E); QMJ7983, Mary Vale Stn, Yalleroi via Blackall (23°35'S 146°58'E); QMJ36794, E of Comer Stn (23°37'S 148°40'E); QMJ34205-06, half way up the Blackdown Tableland escarpment (23°37'S 149°10'E); QMJ8080, Bogantungan (23°39', 147°18'); QMJ741, Diamantina Lakes (23°46'S 141°08'E); QMJ31545, Winton fossil site (23°50'S 142°15'E); QMJ9132, Blackall (24°26'S 145°28'E); QMJ43356-7, Moura, 4km S of junction of Theodore & Gibihi Roads (24°38'S 149°59'E); QMJ7878, QMJ10526, Jundah (24°50'S 143°04'E); QMJ4540, Dawson Valley, Castle Ck (24°50'S 150°20'E); QMJ6011, Weathersfield?; QMJ742, No locality data; AMR128183, Batavia Downs, Wenlock R (12°40'S 142°40'E); AMR128796, Cairns (16°55'S 145°46'E); AMR31773, Mt Fox nr Ingham (18°19'S 145°51'E); AMR113852, approx. 14.5km W of 'Mt Cooper', nr St Paul's vine scrub (20°31'S 146°55'E); AMR14183, 210km S of Charters Towers (21°38'S 146°55'E); AMR63065, approx. 48km NW of Clermont (22°25'S 147°23'E); AMR107703 N of Clermont (22°50'S 147°38'E); AMR120094, Mayne Junction Hotel, approx. 40km N of Diamantina Lakes Stn (23°33'S 141°22'E); AMR15107, Yamala (23°35'S 148°22'E); AMR113116, Diamantina Lakes Stn, SW of Winton (23°41'S 141°11'E); AMR55786, Duaringa (23°43'S 149°40'E); AMR110544, AMR110562,

camp, 14km NE of Scott's Tank, Diamantina Lakes, NW of Windorah (23°45'S 141°40'E); AMR130721-2, AMR130726, 20km W of Moura on Bauhinia Downs road (24°37'S 149°47'E); NMVD7527, Mt Cook, Cooktown (15°28'S 145°15'E); NMVD2040, Queensland, SAMR14023, 22km NW of Cooktown (15°25'S 145°04'E); SAMR12594, Cooktown (15°28'S 145°15'E); SAMR15791, Charters Towers (20°05'S 146°16'E); SAMR1771, Mt Coolon (21°23'S 147°20'E); SAMR42600, 6km N of Diamantina Stn (23°43'S 141°08'E); SAMR42601-02, 4km N of Diamantina Stn (23°44'S 141°08'E); SAMR42603, 85km W of Windorah (25°21'S 141°50'E); WAMR55475-7, 16km W of Charters Towers (20°08'S 146°07'E); WAMR55552, WAMR55601-2, Fermoy Homestead, 88km S of Winton (23°10'S 143°02'E); NTMR1144, Clermont (22°50'S 147°38'E); NTMR266, Rockhampton (23°22'S 150°32'E).

DIAGNOSIS

N. asper is medium-sized and moderately spinose. It is distinguished from *N. sheai* by the colour pattern of its digits (digits unbanded vs digits strongly marked with alternating bands of brown and white); from *N. sheai* and *N. amyaie* by its smaller size (max SVL 114mm vs 121mm *N. sheai*, 135mm *N. amyaie*). It is further distinguished from *N. amyaie* by the spinosity of the its rump and thighs (moderately spinose vs extremely spinose). The arrangement of the basal scales surrounding the tubercles on the rump and thighs also separates *N. asper* and *N. amyaie*. In *N. asper* the basal scales are uniform in size and less than half the height of the central scale. In *N. amyaie* the basal scales are irregular in size and in most specimens examined, some of the basal scales are greater than half the height of the central scale.

In the KS2 analysis *N. asper* (excluding broad-banded CYP specimens which are not significantly separable from other QLD populations of this species) and *N. amyaie* show significant separation of the shape of frequency distributions for; KW, HW, S, NL, R, & I. *N. asper* (excluding broad-banded CYP specimens) and *N. sheai* show significant separation of the shape of frequency distributions for; T, TV, KW, TA, NL, SL, IL & I (Table 1).

DESCRIPTION

SVL(mm): 47-114 (N 74, mean 84.1). Proportions(%SVL): - L1 - 36.8-47.8 (N 74, mean 43.0), L2 - 43.2-55.6 (N 73, mean 49.0), AG - 34.4-54.2 (N 74, mean 44.4), T - 11.4-22.2 (N 66,

TABLE 3. Fisher linear discriminant function coefficients. Animals are assignable to the species with the highest function, given their measurements corrected for SVL.

| char | GROUPS | | | |
|-------|---------|---------|---------|---------|
| | 1 | 2 | 3 | 4 |
| HW | 841.13 | 841.40 | 785.09 | 881.74 |
| I | -26.45 | -134.19 | -116.54 | 95.68 |
| L1 | 372.24 | 330.65 | 361.47 | 314.64 |
| NL | 36.29 | 67.61 | 33.14 | 47.55 |
| R | -37.54 | -12.84 | -56.61 | -50.85 |
| SL | 89.71 | 52.31 | 64.69 | 27.21 |
| TA | -135.06 | -18.37 | -28.78 | 23.92 |
| TV | -3.45 | 47.62 | 54.14 | 48.57 |
| Coast | -197.58 | -193.83 | -184.77 | -195.18 |

mean 16.4), TV - 15.7-27.4 (N 66, mean 22.7), HL - 27.9-34.8 (N 73, mean 31.3), HW - 23.9-30.6 (N 74, mean 27.7), HD - 10.7-15.8 (N 70, mean 13.8), S - 9.2-12.7 (N 74, mean 11.1), EE - 10.0-15.0 (N 73, mean 12.3), NL - 10.4-21.1 (N 72, mean 15.5).

Head. Large and deep, covered with small, round to hexagonal, juxtaposed scales. Posteriorly bearing scattered tubercles intermixed with the smaller scales. Each tubercle consists of a high central scale, circled by a ring of smaller basal scales. Tubercles most prominent on the nape. Dorsal skin co-ossified with skull. Nostril small, opening upwards and backwards. Eye large with vertical pupil. Ear vertically elongate, tympanum deeply recessed. Rostral scale small, with 8-17 (N 77, mean 12.5) scales in direct contact with dorsal edge. Interorbital scales 7-12 (N 76, mean 8.9). Supralabial scales 11-17 (N 152, mean 13.5). Infralabial scales 10-17 (N 152, mean 13.5).

Neck. Broad, less than half width of head.

Body. Stout, dorsal and ventral surfaces with small granular scalation. Granular scales intermixed with larger conical tubercles on dorsal and lateral surfaces. Mid-dorsal tubercles small.

TABLE 4. Classification results for 149 animals. Actual group by predicted group membership.

| Actual Group | No. of Cases | Predicted Group Membership | | | |
|--------------|--------------|----------------------------|----|----|---|
| | | 1 | 2 | 3 | 4 |
| Group 1 | 59 | 45 | 8 | 4 | 2 |
| Group 2 | 48 | 2 | 30 | 7 | 9 |
| Group 3 | 31 | 2 | 2 | 25 | 2 |
| Group 4 | 11 | 0 | 2 | 1 | 8 |

rump tubercles moderate. Basal scales surrounding rump tubercles uniform and less than half as high as the central scale. Rump tubercles larger than flank tubercles (45% material examined) or subequal to flank tubercles (55% material examined). Rump tubercles smaller than nape tubercles (51% material examined) or subequal to nape tubercles (49% material examined). Lower flanks and ventral surface with scattered, slightly raised rosettes which vary between being pronounced or barely discernible.

Limbs. Long and slender, bearing enlarged tubercles on dorsal surfaces. Tubercles on thighs largest, with uniform basal scales less than half as high as the central scale. Digits short, cylindrical, undilated distally and terminating in a non-retractile claw. Third toe on hindlimb longest.

Tail. Short, moderately depressed, constricted at base and terminating in a globular, kidney-shaped knob (KW 17.8–38.8%T, N 66, mean 29.1). Usually four, rarely five or six longitudinal rows of tubercles present on dorsal and lateral surfaces. Uniform basal scales surrounding caudal tubercles less than half as high as the central scale. Caudal annuli 9–12 (N68, mean 10.4).

PATTERN

Body. In spirit, mid-dark brown, or mid-dark grey on dorsal surface. Many specimens have a broad black band on the nape. Seven – eight, rarely six, narrow irregular crossbands (crossbands broad and continuous in CYP specimens) present between head and hindlimbs. Crossbands range from obscure to bold and are continuous or broken into a series of spots, with each spot covering a tubercle. Fine black lines form reticulations which become obscure in larger specimens and can be difficult to see in darker individuals. Ventral surface cream, sometimes faintly marbled with grey or brown.

Limbs. Lacking irregular crossbands distally. Digits unbanded or only obscurely banded.

Tail. As for body, with an obscure, broad, pale crossband on proximal half.

Head. Sometimes slightly lighter than body. Covered dorsally and laterally with fine black reticulations, which form an intricate pattern. These reticulations are most prominent in juveniles and may fade in larger specimens.

DISTRIBUTION

From the drier parts of coastal MEQ through central and western districts. Also present on CYP (Fig. 3).

The locality given for QMJ2125 is 'Northern Rivers', which usually refers to an area in northern NSW. The following entry in the register (QMJ2126) is a specimen of *Saltuarius cornutus* from the same locality. Neither of these species occur in NSW, nor are they sympatric elsewhere. *N. asper* typically occurs in dry open country while *S. cornutus* is confined to rainforest habitats. Either the locality 'Northern Rivers' should be regarded as an error or it refers to a region (unknown to the authors) of southern Cape York Peninsula where both rainforest and dry forests occur.

HABITAT

N. asper favours rocky substrates in open woodlands (Steve Wilson, Tim Hawkes, pers. comm.). It has been recorded also from stony or compacting soil plains, where sheltering sites are available (Ehmann 1992; Couper, unpubl. data); from low heath at Heathlands, CYP, and Darwin Stringybark open forest, at Aurukun (Cameron & Cogger, 1992).

REPRODUCTIVE NOTES

Clutch size - two eggs. Egg-laying occurs in mid-late summer. Female WAMR55476 was gravid during late February. The two oviducal eggs measured 27.1 X 13.8mm and 25.2 X 14.0mm; QMJ54644 had a greatly enlarged vitellogenic follicle in each ovary at the time it was killed in early February, 1992. The largest of these measured 9.67 X 7.28mm. A gravid female was brought to Wild World for identification in mid-April (T. Hawkes, pers. comm.). Male WAMR55552 was in reproductive condition (epididymis enlarged and turgid) in late November.

DIETARY NOTES

The gut of QMJ56088 contained two cricket legs (Orthoptera: Gryllidae). QMJ36795 contained a medium-sized centipede (Chilopoda: Scolopendridae) and an ant. QMJ44689 contained fragments of a medium-sized spider, and a medium-sized cockroach (Blattodea: Blattidae). Two faecal samples were collected at Heathlands, CYP, in late January 1992. The first sample contained a large spider, a small centipede, a large coleopteran larva and small to medium-sized cockroaches (Blattodea). The second sample

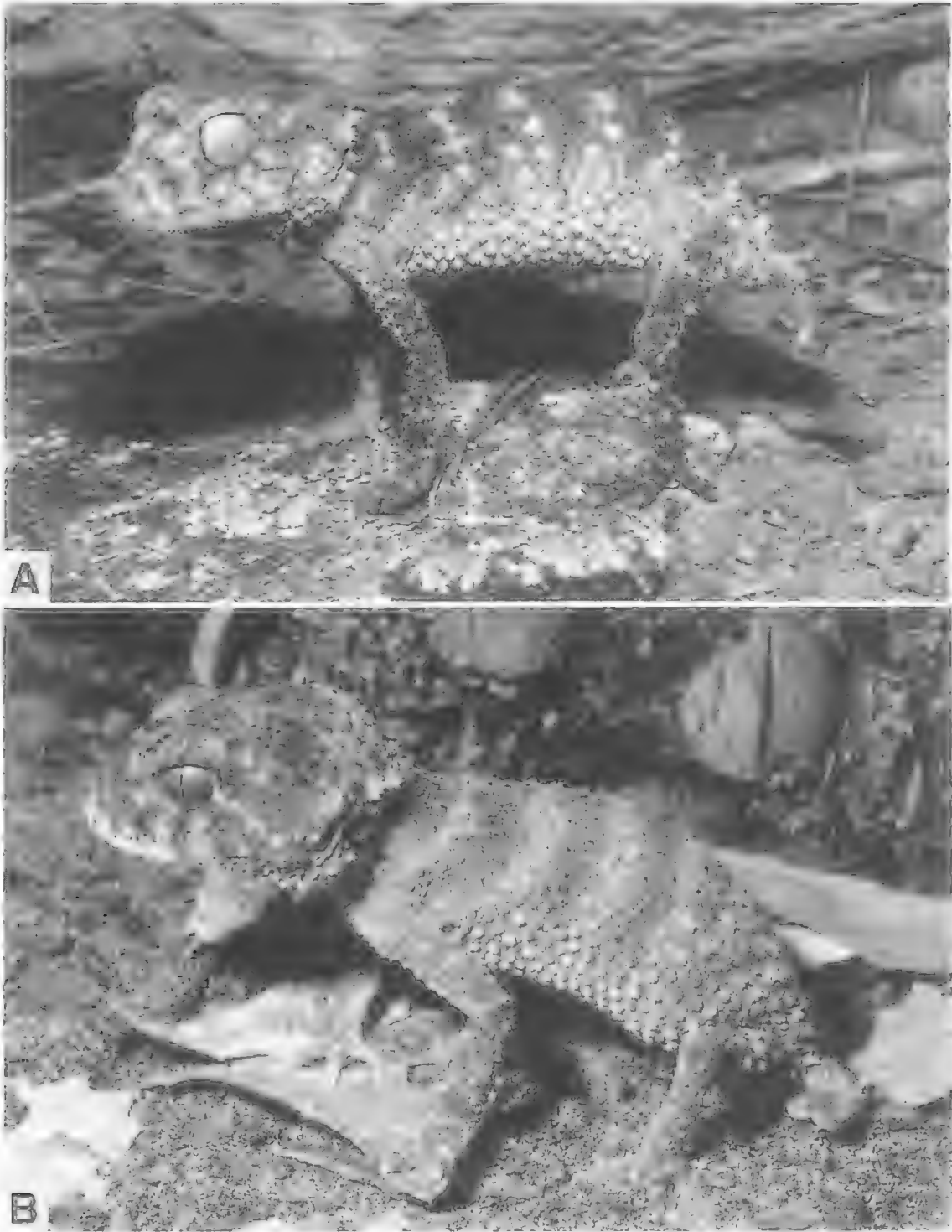


FIG. 2. *Nephurus asper*. A, Moura, QLD; B, Broad-banded form, Heathlands, Cape York Peninsula, QLD. (Photographs: S. Wilson).

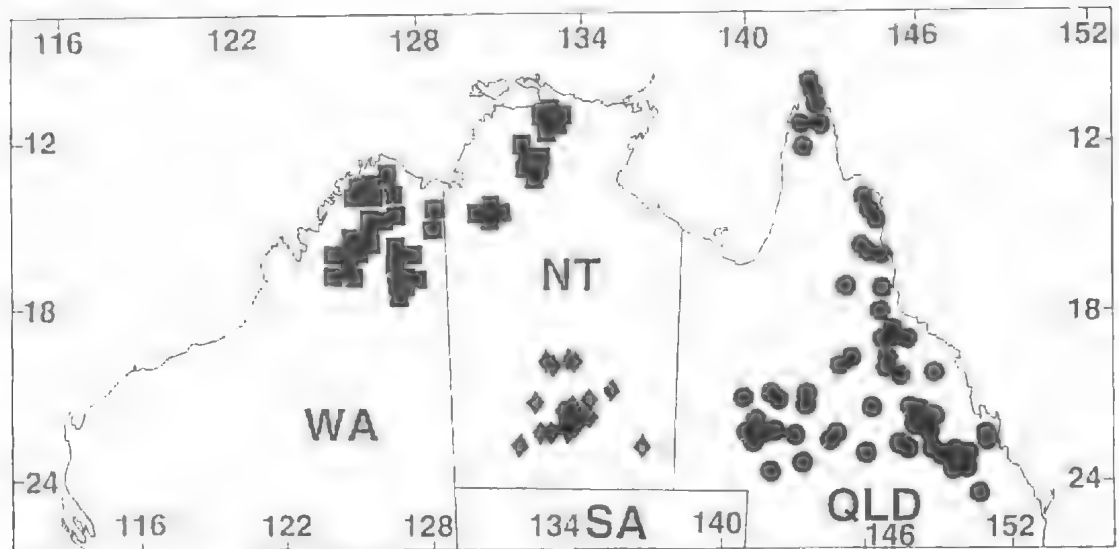


FIG. 3. Distribution of the *Nephurus asper* species complex. *N. amya* (diamonds), *N. asper* (circles), *N. sheai* (squares).

contained legs from a medium-sized grasshopper (Acrididae), fragments of a large scorpion (*Urodacus* sp.) and fragments of a small phasmid.

REMARKS

A clear photograph of the holotype of *N. asper* (BMNH1946.8.23.34) was provided by Bauer, (1990). The narrow, irregular dorsal crossbands and moderate, uniform rump scalation of this specimen are consistent with the pattern and scalation of QMJ56088, a specimen recently collected only 14km from the type locality. Further, these specimens are morphologically/phenotypically consistent with populations of spinose *Nephurus* occurring in Queensland between 18°19'S & 25°21'S. These are regarded here as *N. asper*. The broad-banded form on CYP is also included in *N. asper* because it cannot be significantly separated from this species by scalation features or body proportions, and preliminary genetic data show a low level of divergence between a specimen from Heathlands, CYP and a specimen from the Capella region of MEQ (Couper & Donnellan, unpubl. data).

The broad-banded CYP colour form is narrowly separated from the narrow-banded form at the southern limit of its range. Tim Hawkes (Cape York Herpetological Society) has provided colour transparencies of a broad-banded specimen from 6km east of Almaden (17°21'S, 144°43'E) and a narrow-banded specimen from approximately 87km south, near the junction of the Kennedy and Gulf Redevelopmental High-

ways (18°09', 144°41'). This narrow-banded specimen is approximately 75km NE of the most southerly museum record of the broad-banded form (QMJ57993). Clearly, the range of both colour forms overlap latitudinally but, to date, they have not been found in sympatry.

Nephurus amya Couper sp. nov. (Fig. 4; Statistical analyses group 3)

Nephurus asper; Cogger, 1992 (in part).

MATERIAL EXAMINED

HOLOTYPE: AMR104458, Winnecke Goldfields, Garden Stn, N of Alice Springs, NT (23°17'S 134°25'E). Found in mine tunnel, February, 1982. Don. M. Robinson.

PARATYPES: NORTHERN TERRITORY: QMJ51650, 15km SE of Glen Helen (23°31'S 132°21'E); QMJ53650, Hugh R, nr Alice Springs (23°49'S 133°22'E); AMR49716, Mt Gillen, Alice Springs (23°42'S 133°48'E); AMR50542, Alice Springs (23°42'S 133°53'E); AMR11965, Mt Gillen, Alice Springs (23°43'S 133°48'E); AMR90198, Jay Ck, NT (23°50'S 133°29'E); AMR10371, between Hale and Plenty Rivers, Central Australia (24°25'S 136°10'E); NMVD538, Barrow Ck, (21°32'S 133°53'E); NMVD51919-21, 28.9km S of Barrow Ck (21°45'S 133°40'E); NMVD55377, nr Alice Springs (23°42'S 133°52'E); NMVD12684-5, Central Australia; SAMR1892, Barrow Ck (21°32'S 133°53'E); SAMR38837, Mt Zeil (23°25'S 132°25'E); SAMR40561, approx 35km SE of Kings Ck Homestead (24°26'S 131°49'E); SAMR30523, No Locality data; NTMR441, Barrow Ck (21°32'S 133°53'E);

R14096, Mt Riddock Stn, Dulcie Ra. (22°30'S 135°25'E); NTMR33717, Winnecke Goldfields (23°02'S 134°23'E); NTMR33716, Bond Springs Stn (23°34'S 133°52'E); NTMR12377, 16km N Alice Springs (23°34'S 133°53'E); NTMR33720, Alice Springs Hills, 19 Mile Bore (23°35'S 133°52'E); NTMR33722-3, Alice Springs, Wigleys Turnoff (23°36'S 133°53'E); NTMR12380, 9km N Alice Springs (23°37'S 133°53'E); NTMR33721, Alice Springs, Charles R (23°39'S 133°51'E); NTMR5586, NTMR5969, NTMR14991, Alice Springs (23°42'S 133°52'E); NTMR33724, NTMR33726, Alice Springs (23°42'S 133°53'E); NTMR5383, Alice Springs Power House (23°42'S 133°55'E); NTMR5466, Alice Springs, Mt Gillen (23°43'S 133°48'E); NTMR2458, Alice Springs, Emily Gap (23°45'S 133°57'E); NTMR33719, Hermannsburg, Finke Crossing (23°58'S 132°46'E); NTMR33715, Krichauff Ra. (23°59'S 132°38'E); NTMR33728, No data.

DIAGNOSIS

N. amylae is the largest and most spinose member of the *N. asper* species group. Its large size distinguishes it from other members of this group (max SVL 135mm vs 114mm *N. asper*, 121mm *N. sheai*). It is further distinguished from *N. asper* and *N. sheai* by the spinosity of the its rump and thighs (extremely spinose vs moderately spinose). The arrangement of the basal scales surrounding the tubercles on the rump and thighs also separates *N. amylae* from *N. asper* and *N. sheai*. In *N. amylae* the basal scales are irregular in size and in most specimens examined, some of the basal scales are greater than half the height of the central scale. In *N. asper* and *N. sheai* the basal scales are uniform in size and less than half the height of the central scale.

In the KS2 analysis *N. amylae* and *N. asper* (excluding broad-banded CYP specimens which are not significantly separable from other QLD populations of this species) show significant separation of the shape of frequency distributions for; KW, HW, S, NL, R & I. *N. amylae* and *N. sheai* show significant separation of the shape of frequency distributions for; KW, HW, HL, S, NL, SL, IL, R & I (Table 1).

DESCRIPTION

SVL(mm): 50-135 (N 40, mean 100.3). Proportions, (%SVL): - L1 - 38.1-52.4 (N 40, mean 42.7), L2 - 42.5-56.1 (N 40, mean 48.4), AG - 35.4-53.5 (N 40, mean 45.1), T - 12.3-17.5 (N 37, mean 15.0), TV - 15.2-25.2 (N 37, mean 21.3), HL - 27.7-34.2 (N 38, mean 30.4), HW - 23.9-30.6 (N 38, mean 26.4), HD - 10.5-15.1 (N 38, mean 13.2), S - 9.1-12.9 (N 39, mean 10.5), EE -

10.2-14.8 (N 39, mean 12.9), NL - 10.4-19.9 (N 37, mean 14.7).

Head. Large and deep, covered with small, round to hexagonal, juxtaposed scales. Posteriorly bearing scattered tubercles intermixed with the smaller scales. Each tubercle consists of a high central scale, circled by a ring of smaller basal scales. Tubercles most prominent on the nape. Dorsal skin co-ossified with skull. Nostril small, opening upwards and backwards. Eye large with vertical pupil. Ear vertically elongate, tympanum deeply recessed. Rostral scale small, with 7-18 (N 39, mean 9.7) scales in direct contact with dorsal edge. Interorbital scales 6-11 (N 40, mean 8.0). Supralabial scales 11-17 (N 78, mean 13.5). Infralabial scales 11-17 (N 78, mean 13.4).

Neck. Broad, less than half width of head.

Body. Stout, dorsal and ventral surfaces with small granular sculation. Granular scales intermixed with larger conical tubercles on dorsal and lateral surfaces. Mid-dorsal tubercles small, rump tubercles large (extremely pronounced) except in juveniles. Basal scales surrounding rump tubercles irregular. In many specimens, some are greater than half the height of the central scale. Rump tubercles larger than flank tubercles. Rump tubercles larger than nape tubercles (90% material examined) or subequal to nape tubercles (10% material examined). Lower flanks and ventral surface with scattered, slightly raised rosettes which vary between being pronounced or barely discernible.

Limbs. Long and slender, bearing enlarged tubercles on dorsal surfaces. Tubercles on thighs largest (extremely pronounced). Basal scales surrounding thigh tubercles irregular. In many specimens some are greater half the height of the central scale. Digits short, cylindrical, undilated distally and terminating in a non-retractile claw. Third toe on hindlimb longest.

Tail. Short, moderately depressed, constricted at base and terminating in a globular, kidney-shaped knob (KW 21.3-35.0 %T, N 36, mean 27.6). Four longitudinal rows of tubercles present on dorsal and lateral surfaces. Basal scales surrounding caudal tubercles less than half the height of the central scale. Caudal annuli 8-13 (N 37, mean 10.4).

The measurements and scale counts for the holotype (AMR104458) are as follows; SVL 135.0mm, L1 54.1mm, L2 63.1mm, T 19.4mm, TV 23.3mm, HL 40.0mm, HW 34.4mm, HD 17.4mm, S 12.8mm, EE 18.4mm, NL 14.9mm, KW 4.5mm, R 8, I 7, SL 15/15, IL 14/14, TA 10.



FIG. 4. *Nephruroides amylae*. Kings Ck Stn, southwestern NT. (Photograph: S. Wilson).

This species has been illustrated previously as *N. asper* (e.g. Hoser, 1989: 74).

PATTERN

Body. In spirit, fawn to mid brown on dorsal surface. Many specimens with a black band present on the nape. Some specimens with seven to nine obscure, broken crossbands. These appear as a series of spots with each spot covering a tubercle. Others with no indication of banding or with obscure blotches along the vertebral line. Fine black lines form a reticulated pattern on the dorsum and upper lateral zone. These lines fade in larger specimens. Ventral surface cream.

Limbs. Lacking irregular crossbands distally. Digits unbanded but sometimes obscurely mottled.

Tail. As for body, with an obscure, broad, pale crossband on proximal half.

Head. Often paler than body. Covered on top and sides with fine black reticulations which form an intricate pattern. These fade in larger specimens.

ETYMOLOGY

For Amy Couper.

DISTRIBUTION

Confined to the hill country of the south-central NT centred around Alice Springs (23°42'S, 133°53'E), extending north to Barrow Ck (21°32'S, 133°53'E) (Fig. 3).

HABITAT

N. amylae favours open ground on rocky substrates in open woodland habitats. It may be found associated with a scattered *Triodia* ground-cover.

REPRODUCTIVE NOTES

Clutch size two eggs. Females (NTMR33722-23, NTMR5466) had small vitellogenic follicles on their ovaries between mid October - late December (<5.5mm diameter). NTMR2458, collected in mid March, had a greatly enlarged follicle in each ovary (the largest of these follicles measured 14.58mm × 13.0mm). Bedford and Christian (1993) provide clutch data for a specimen from Gardens Station, 75km northeast of Alice Springs. Two eggs measuring 34.3mm × 16.6mm and 37.0mm × 16.1mm were laid on the 17/18 February 1992. These weighed 5.6g

and 5.8g respectively. The total clutch was 24.8% of the non-gravid female mass.

Three males (NTMR33719, NTMR33721 & NTMR441) collected between early October - late November appeared to be in reproductive condition (epididymis enlarged and turgid).

DIETARY NOTES

The gut of NTMR33723 contained a large centipede (Chilopoda: Scolopendridae), as did QMJ51650. QMJ53650 contained an ant head (Hymenoptera: Formicidae), the hind legs of a grasshopper (Orthoptera: Acrididae) and many medium-sized cockroach fragments (Blattodea: Blattellidae).

REMARKS

N. amya is one of Australia's largest geckos in terms of SVL and weight (max SVL 135mm, AMR104458). It is exceeded in length only by *Saltuarius cornutus* (max SVL 145mm) and *S. salebrosus* (max SVL 141mm). However, despite its greatly reduced tail size, it is substantially heavier than both of these species and weighs a maximum of 65g (AMR104458). AMR104458 was compared in weight to a number of other large Australian gecko species held in the AM and QM collections. The results are as follows: *Carphodactylus leavis* QMJ54312 (SVL 107mm, weight 26g); *Cyrtodactylus louisianensis* QMJ38198 (SVL 130mm, weight 46g); *Rhacodactylus australis* QMJ39723 (SVL 110mm, weight 27g); *Saltuarius cornutus* QMJ48179 (SVL 140mm, weight 49g), QMJ30991 (SVL 137mm, weight 57g), AMR42163 (SVL 145mm, weight 43g); *S. salebrosus* QMJ22288 (SVL 141mm, weight 57g) and *S. swaini* QMJ51640 (SVL 131mm, weight 43g).

Nephrurus sheai Couper sp. nov.
(Fig. 5; Statistical analyses group 1)

Nephrurus asper, Cogger, 1992 (in part).

MATERIAL EXAMINED

HOLOTYPE: NTMR11470, Bowerbird Camp, Magela Ck, NT (12°47'S 133°07'E), coll. I. Archibald and J. Bywater, 01 September, 1983.

PARATYPES: QMJ52872, March Fly Glen, Gibb R Rd, Kimberley, WA; QMJ57515, 10km SE of Oenpelli, NT (12°22'S 133°07'E); AMR93181, Jabiluka Project area, NT (12°29'S 132°54'E); AMR93182, Jabiluka Project area, NT (12°31'S 132°57'E); AMR88668, Jabiluka Project area, NT (12°34'S 132°55'E); AMR13403, Katherine, NT (14°28'S 132°16'E);

AMR12876, Manbullo Stn, NT (14°31'S 132°12'E); AMR72980, Jasper Gorge, NT (16°02'S 130°40'E); AMR140279, Manning Gorge, Mt Barnett Stn, WA (16°39'31"S 125°55'37"E); NMVD4552, Pine Ck, NT (13°49'S 131°50'E); SAMR3597, Moolabulla, WA (18°12'S 127°30'E); WAMR13646, WAMR27374, Kalumburu, WA (14°18'S 126°38'E); WAMR47587, 8km N of Katherine, NT (14°25'S 132°12'E); WAMR43153, WAMR77269, WAMR77581, WAMR77585 Mitchell Plateau, WA (14°49'S 125°50'E); WAMR56423, King Edward R Crossing, WA (14°52'S 126°12'E); WAMR50460, Drysdale R NP, WA (15°09'S 127°06'E); WAMR46782, Prince Regent R, WA (15°19'S 125°35'E); WAMR73903, Ellenbrae Stn, WA (15°57'S 127°04'E); WAMR60343, WAMR60947, Jasper Gorge 53km NW of Victoria River Downs Homestead, NT (16°02'S 130°41'E); WAMR60362, Jasper Gorge 53km NW of Victoria River Downs, NT (16°02'S 130°45'E); WAMR57123-7, Gibb R Crossing 47km N of Gibb River Stn, WA (16°06'S 126°31'E); WAMR52661, WAMR86927, Lake Argyle (Ord R), WA (16°07'S 128°44'E); WAMR83359, 24km NW of Mt Elizabeth Homestead, WA (16°11'S 126°00'E); WAMR70562, 3.5km at 288° from (new) Lissadell Homestead, WA (16°39'S 128°31'E); WAMR73904, Mt Barnett Stn, WA (16°40'S 125°57'E); WAMR56466, Plain Ck, Beverley Springs Stn, WA (16°43'S 125°23'E); WAMR83531-2, Galvans Gorge, WA (16°48'S 125°51'E); WAMR64731, 4.5km at 140° from Clancys Yard, WA (17°07'S 125°35'E); WAMR70551, 9.5km at 256° from Inglis Gap, WA (17°07'S, 125°05'E); WAMR57118, Inglis Gap, King Leopold Range, WA (17°08'S 125°10'E); WAMR70552, 8.6km at 167° from Mt Amy (Napier Downs Stn), WA (17°14'S 124°54'E); WAMR58671, 20km ENE of Tableland, WA (17°14'S 127°01'E); WAMR58636, 25km SE of Bedford Downs Homestead, WA (17°27'S 127°36'E); WAMR58647, 10km SE of Lansdowne Homestead, WA (17°41'S, 126°48'E); WAMR1340, Leopold Downs, WA (17°52'S 125°25'E); WAMR12614, Calwynyardah, WA (18°00'S 124°47'E); WAMR70029, 43km at 316° from Fitzroy Crossing P.O., WA (18°00'S 125°30'E); WAMR48175, Moola Bulla, WA (18°11'S 127°30'E); WAMR26633, Halls Ck, WA (18°13'S 127°39'E); WAMR87092, 8km SW of Halls Ck, WA (18°16'S 127°37'E); WAMR46116, Margaret River Homestead, WA (18°38'S 126°57'E); WAMR87082, 0.5km N of Mary Pool, WA (18°43'S 126°53'E); NTMR12605, Nabarlek, NT (12°19'S 133°19'E); NTMR17822, 10km SE Oenpelli, NT (12°22'S 133°07'E); NTMR12493, Magela Ck, Bowerbird Camp, NT (12°47'S 133°05'E); NTMR11464, Magela Ck, Bowerbird Camp, NT (12°47'S 133°07'E); NTMR4027, NTMR4272, Jim Jim Falls, NT (13°17'S 132°50'E); NTMR387, Katherine, 4.7mi N, NT (14°27'S 132°15'E); NTMR3759-61, Katherine, 4km N, NT (14°27'S 132°15'E); NTMR267, NTMR297, Katherine, NT (14°28'S 132°16'E); NTMR2377, Katherine, Lower Farm Rd, NT (14°35'S 132°12'E); NTMR33718,



FIG. 5. *Nephurus sheai*. Manning Gorge, Gibb R Track, Kimberley region, WA. (Photograph: G. Harold).

Wickham R, Victoria River Downs, NT (16°05'S 130°35'E); NTMR13485, Gregory NP, Bullita area, NT (16°07'S 130°26'E).

DIAGNOSIS

N. sheai is a large, moderately spinose member of the *N. asper* species group. *N. sheai* is distinguished from *N. asper* and *N. amyaie* by the colour pattern of its digits (digits strongly marked with alternating bands of brown and white vs digits not strongly banded with brown and white); also by size (max SVL 121mm vs 114mm *N. asper*, 135mm *N. amyaie*). It is further distinguished from *N. amyaie* by the spinosity of the its rump and thighs (moderately spinose vs extremely spinose). The arrangement of the basal scales surrounding the tubercles on the rump and thighs also separate *N. sheai* and *N. amyaie*. In *N. sheai* the basal scales are uniform in size and less than half the height of the central scale. In *N. amyaie* the basal scales are irregular in size and in most specimens examined, some of the basal scales are greater than half the height of the central scale.

In the KS2 analysis *N. sheai* and *N. amyaie* show significant separation of the shape of frequency distributions for; KW, HW, HL, S, NL, SL, IL, R &

I. *N. sheai* and *N. asper* (excluding broad-banded CYP specimens which are not significantly separable from other QLD populations of this species) show significant separation of the shape of frequency distributions for; T, TV, KW, TA, NL, SL, IL, & I. (Table 1).

DESCRIPTION

SVL(mm): 42.3-121.4 (N 69, mean 82.8). Proportions, (%SVL): - L1 - 37.9-50.7 (N 69, mean 44.0), L2 - 45.0-59.1 (N 69, mean 49.8), AG - 35.2-52.4 (N 67, mean 43.9), T - 10.1-21.7 (N 68, mean 14.8), TV - 14.1-26.4 (N 68, mean 19.8), HL - 28.4-34.3 (N 68, mean 31.2), HW - 23.6-31.7 (N 69, mean 27.5), HD - 11.0-16.1 (N 69, mean 13.6), S - 9.4-13.0 (N 69, mean 11.0), EE - 10.9-15.1 (N 69, mean 12.8), NL - 8.6-18.0 (N 68, mean 14.6).

Head. Large and deep, covered with small, round to hexagonal, juxtaposed scales. Posteriorly bearing scattered tubercles intermixed with the smaller scales. Each tubercle consists of a high central scale, circled by a ring of smaller basal scales. Tubercles most prominent on the nape. Dorsal skin co-ossified with skull. Nostril small, opening upwards and backwards. Eye

large with vertical pupil. Ear vertically elongate, tympanum deeply recessed. Rostral scale small, with 7-18 (N 69, mean 12.4) scales in direct contact with dorsal edge. Interorbital scales 8-15 (N 66, mean 10.5). Supralabial scales 12-20 (N 138, mean 15.8). Infralabial scales 11-20 (N 137, mean 16.1).

Neck. Broad, less than half width of head.

Body. Stout, dorsal and ventral surfaces with small granular scalation. Granular scales intermixed with larger conical tubercles on dorsal and lateral surfaces. Mid-dorsal tubercles small, rump tubercles small to large. Basal scales surrounding rump tubercles uniform, less than half as high as the central scale. Rump tubercles larger than flank tubercles (85% material examined) or subequal to flank tubercles (15% material examined). Rump tubercles smaller than nape tubercles (41% material examined) or subequal to nape tubercles (59% material examined). Lower flanks and ventral surface with scattered, slightly raised rosettes which vary between being pronounced or barely discernible.

Limbs. Long and slender, bearing enlarged tubercles on dorsal surfaces. Tubercles on thighs largest, with uniform basal scales less than half as high as the central scale. Digits short, cylindrical, undilated distally and terminating in a non-retractile claw. Third toe on hindlimb longest.

Tail. Short, moderately depressed, constricted at base and terminating in a globular, kidney-shaped knob (KW 21.2-47.9 %T, N 67, mean 31.5). Four longitudinal rows of tubercles present on dorsal and lateral surfaces. Basal scales surrounding caudal tubercles uniform and less than half as high as the central scale. Caudal annuli 8-12 (N69, mean 9.7).

The measurements and scale counts for the holotype (NTMR11470) are as follows: SVL 106.8mm, L1 45.3mm, L2 52.5mm, T 15.5mm, TV 21.4mm, HL 32.5mm, HW 29.8mm, HD 13.3mm, S 10.9mm, EE 14.3mm, NL 17.4mm, KW 4.6mm, R 13, I 11, SL 18/17, IL 16/15, TA 11.

This species has been illustrated previously as *N. asper* (e.g. Storr et. al., 1990: 82, pl.1; Schmida, 1985: 103).

PATTERN

Body. In spirit, tan - greyish brown on dorsal surface. Many specimens have a broad black band on the nape. Seven - 11 narrow, irregular, cream crossbands present between head and hindlimbs. Crossbands range from obscure to

bold and are continuous or broken into a series of spots, with each spot covering a tubercle. In most specimens fine black lines lie between the cream crossbands. These black lines are sometimes interconnected to form a reticulated pattern. Ventral surface cream, sometimes faintly marbled with grey or brown.

Limbs. Often with irregular crossbands on the distal half. Digits heavily banded with brown and white.

Tail. As for body, with an obscure, broad, pale crossband on proximal half.

Head. Tan, usually paler than the body. Covered dorsally and laterally with fine black reticulations which form an intricate pattern. These lines are most prominent in juveniles and may fade in larger specimens.

ETYMOLOGY

For Glenn Shea.

DISTRIBUTION

Confined to hill country from the Kimberley Region of WA to the Arnhem Escarpment in the NT (Fig. 3).

HABITAT

N. sheai favours rocky substrates in open woodland habitats. It is frequently associated with a scattered *Triodia* ground-cover (G. Harold, pers. comm.). The holotype (NTMR11470) was collected from a rocky outcrop in mid-high open forest with a grass understorey.

REPRODUCTIVE NOTES

Clutch size - usually two eggs, although a single egg clutch has been recorded (How et. al., 1990). Gravid females are present in the population in January - WAMR86927, WAMR27374; February - WAMR87092 and June - NTMR33718. WAMR70551 had a greatly enlarged vitellogenic follicle (12.42 × 10.83mm) in the ovary in May. Incubation of the eggs takes 115 days at a mean temperature of approximately 25°C (Ehmann, 1992). Gow, 1979 recorded the measurements of two eggs laid on 5 Dec 1973 (30 × 16.5mm and 29 × 15.5mm). Males were in reproductive condition (epididymis enlarged and turgid) in November - WAMR56423, NTMR267 and in February - WAMR48175. How et al. (1990), record reproductive activity extending over at least nine months (spanning the October-April wet period) for *N. sheai* in WA and suggest that reproductive activity may occur throughout the year.

DIETARY NOTES

The gut of QMJ57515 contained moth or caterpillar cuticle with dense, short hairs. QMJ52872 contained numerous termite heads (*Nasutitermes* sp.).

REMARKS

AMR125387 was collected from Cadell Ck, near Hamilton, western QLD. This specimen has strongly banded toes, a diagnostic feature of *N. sheai*. Its occurrence in Queensland is not consistent with the overall distribution pattern of this species. Further, of the QLD material examined in this study (79 \times *N. asper*), AMR125387 is the only specimen to possess strongly banded toes. Because of these inconsistencies, this specimen has not been included in the material examined for either *N. sheai* or *N. asper*. The status of this specimen is uncertain. We believe there has been an error with the collection data.

KEY TO *N. ASPER* SPECIES COMPLEX

1. Digits strongly banded brown and white
..... *N. sheai*
 Digits not strongly banded 2
2. Tubercles of the rump and thighs extremely pronounced,
 usually much larger than those covering the rest of the
 dorsum *N. amiae*
 Tubercles of the rump and thighs small to
 moderate *N. asper*

ACKNOWLEDGEMENTS

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AN EARLY FLECKER RADIOGRAPH OF *HYDROPHIS ELEGANS*, AND NEW INFORMATION ON ITS FEEDING HABITS. *Memoirs of the Queensland Museum* 37(1):68.1994;- Dr Hugo Flecker (1884-1957) was a prominent naturalist - radiologist who spent much of his life in Cairns, NEQ. His work is widely known. He made large, significant, botanical collections; founded the North Queensland Naturalist's Club; and published extensively on plant and animal injuries to humans. A host of plant and animal species bear the name *fleckeri* in recognition of the value of his contributions to natural history. Flecker was also a pioneer in the field of radiotherapy and published on this, and on early bone development in humans (Clarkson, 1990; Pearn, 1994).

It is not surprising to find that Flecker combined his major interests of natural history and radiology. He took at least 20 radiographs of native animals. These have recently been rediscovered (JRC). Amongst the series of prints (all original films appear to be lost) are radiographs of two species of sea snakes, *Hydrophis elegans* and *Astrotia stokesii*. That of the latter species is insignificant zoologically. However, that of the *H. elegans* specimen provides new data on the feeding habits of this species, and is of aesthetic interest (Fig. 1). Neither of the sea snake radiographs bears a date. However, as others in the series were taken in 1939, it seems reasonable to suggest those of the sea snakes date, at least roughly, from the same era.

The prey species of many sea snakes of Australia's tropical and subtropical waters are well known (e.g. Limpus, 1987). Most are bottom-feeders. Some have ultra-specialized diets (e.g. *Emydocephalus annulatus*, which feeds on only blennioid and gobioid fish eggs from burrows in coral reefs). A few feed on a wide range of animals (e.g. *Aipysurus laevis* eats

fish, prawns, crabs, worms and fish eggs from coral and rock reefs). *H. elegans* is reported to feed solely on very elongate fishes from soft bottom inshore waters (Limpus, 1987).

Flecker's radiograph shows clearly three fish (the posterior-most specimen is a Herring, Family Clupeidae; the others are Cardinal Fish, Family Apogonidae; R. McKay, pers. comm.) and a shrimp (Infraorder Caridea; J. Short, pers. comm.) in the gut of a specimen identified by him as *H. elegans*. This suggests that *H. elegans* may be a less highly specialised feeder than reported to date.

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- J.A. Covacevich, *Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia*; J.H. Pearn, *Department of Child Health, University of Queensland, Royal Children's Hospital, Herston, Queensland 4029, Australia*; J.R. Clarkson, *Queensland Herbarium (Mareeba office), Mareeba, Queensland 4880, Australia*; 20 July 1994.



FIG. 1. Radiograph of *Hydrophis elegans*, following ingestion of two fish and a shrimp. (Dr Hugo Flecker).

TYPE SPECIMENS OF FROG AND REPTILE SPECIES, QUEENSLAND MUSEUM: RECENT ADDITIONS AND NEW INFORMATION

J.A. COVACEVICH AND P.J. COUPER

Covacevich, J.A. & Couper, P.J. 1994 12 01: Type specimens of frog and reptile species, Queensland Museum: recent additions and new information. *Memoirs of the Queensland Museum* 37(1):53-65. Brisbane. ISSN 0079-8835.

Since publication of the last list of frog and reptile type specimens in 1981, types of 25 species of frogs and 78 species of reptiles have been deposited in the Queensland Museum reference collections. In addition, new data are to hand on types of two species of frogs and 14 species of reptiles listed in previous Queensland Museum type lists. □ *Type specimens, frogs, reptiles, Queensland, Australia*.

J.A. Covacevich & P.J. Couper, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 20 August 1994.

The tradition of listing type specimens in the frog and reptile reference collections of the Queensland Museum began over forty years ago (Mack & Gunn, 1953; Covacevich, 1971; Ingram & Covacevich, 1981). Since the last list went to press in June, 1980, there have been many additions to the type collections; a 'lost' holotype has been found; some problems identified in previous lists have been solved; the currently recognised names of several have changed; and there are also some corrections of transcription and other errors.

In recent years, several texts of Australia's frog and reptile species have been published (e.g. Cogger, 1992). From these, it is tempting to see Queensland's species as well known at least to the first level of description and documentation of distribution. However, the rate of discovery and description of new species has been so rapid, that each of these texts has been incomplete at publication. For example, the review of Cogger (1992) is the most recent, and is extremely comprehensive. Yet it does not include one species of frog and 21 species of reptiles described from Queensland since its publication. Between June, 1980 and January, 1995, 22 species of frogs and 72 species of reptiles have been described from Queensland. Almost all are currently recognised.

This list is presented in two parts. In the first, the names are arranged alphabetically by genus and species, in standard phylogenetic order. For each, we provide author/s, date, current status (if there is any variation), registration number, and any necessary explanatory comments. In the second, we document all changes which have been made with names or taxa listed in previous Queensland Museum type lists, in the same order and format.

The following abbreviations have been used: - Australian Museum (AM); Queensland Museum (QM) and Queensland National Parks and Wildlife

Service (QNPWS - now Queensland Department of Environment and Heritage).

FROG AND REPTILE TYPE SPECIMENS DEPOSITED IN THE QUEENSLAND MUSEUM SINCE JUNE 1980

Class AMPHIBIA
Family HYLIDAE

Cyclorana manya
Van Beurden & McDonald, 1980

Holotype QMJ34886; paratypes QMJ34887-88, QMJ36894-900. Data as for type description. Erroneously, QMJ34889 was listed in the type description instead of QMJ34887. The number QMJ34889 is for a specimen of *Uperoleia lithomoda*.

Litoria electrica
Ingram & Corben, 1990

Holotype QMJ38963; paratypes QMJ27240-43, QMJ38964, QMJ38973-74, QMJ38976-77, QMJ49227-28. Data as for type description.

Litoria pallida
Davies, Martin & Watson, 1983

Paratypes QMJ39256-58, QMJ41013-19. Data as for type description.

Litoria revelata
Ingram, Corben & Hosmer, 1982

Holotype QMJ28233; paratypes QMJ10896, QMJ12853, QMJ13156, QMJ19867-69, QMJ19872-73, QMJ19887, QMJ19889-90, QMJ19892-94, QMJ19898, QMJ19900, QMJ19909-12, QMJ19915, QMJ19918, QMJ28232, QMJ30116-35, QMJ30137-

59, QMJ31465, QMJ31467-68, QMJ31971, QMJ35087, QMJ35105-06, QMJ35115-16, QMJ35539, QMJ35543. Data as for type description.

Litoria xanthomera

Davies, McDonald & Adams, 1986

Holotype QMJ42011; paratypes QMJ17109-10, QMJ25194-95, QMJ25258-60, QMJ25278, QMJ27105-06, QMJ35900-03, QMJ35910, QMJ35916, QMJ35919, QMJ35921, QMJ35943-44, QMJ35946, QMJ35950, QMJ35960, QMJ35962-63, QMJ35985-86, QMJ36011, QMJ36020, QMJ36024. Data as for type description.

Nyctimystes oktediensis

Richards & Johnston, 1993

Holotype QMJ56896; paratypes QMJ56897-98. Data as for type description.

Family MICROHYLIDAE

Asterophrys leucopus

Richards, Johnston & Burton, 1994

Holotype QMJ58650. Data as for type description.

Cophixalus bombiens

Zweifel, 1985

Holotype QMJ42060; paratype QMJ42063. Data as for type description.

Cophixalus crepitans

Zweifel, 1985

Holotype QMJ28817; paratypes QMJ41643-53. Data as for type description.

Cophixalus hosmeri

Zweifel, 1985

Holotype QMJ42058; paratypes QMJ37281-83, QMJ56467-91. Data as for type description.

Cophixalus infacetus

Zweifel, 1985

Holotype QMJ42059; paratypes QMJ29728-29, QMJ41639-41. Data as for type description.

Cophixalus mcdonaldi

Zweifel, 1985

Holotype QMJ42064; paratypes QMJ42040-57. Data as for type description.

Cophixalus monticola

Richards, Dennis, Trenerry & Werren, 1994

Holotype QMJ58727; paratypes QMJ58728-33, QMJ58854-57, QMJ58871-74. Data as for type description.

Cophixalus peninsularis

Zweifel, 1985

Holotype QMJ42061; paratype QMJ42062. Data as for type description.

Cophixalus tuberculus

Richards, 1992

Paratype QMJ55246. Data as for type description.

Family MYOBATRACHIDAE

Mixophyes fleayi

Corben & Ingram, 1987

Holotype QMJ26901; paratypes QMJ5198, QMJ26469-70, QMJ27859, QMJ29930-31, QMJ30545-48, QMJ32059, QMJ34101-03, QMJ34243-44, QMJ35461-65. Data as for type description.

Pseudophryne covacevichae

Ingram & Corben, 1994

Holotype QMJ52286; paratypes QMJ53870, QMJ53920-32. Data as for type description.

Pseudophryne raveni

Ingram & Corben, 1994

Holotype QMJ58433; paratypes QMJ1505-06, QMJ2955, QMJ12304, QMJ12310, QMJ12385, QMJ12867, QMJ18699-700, QMJ18702, QMJ18704-05, QMJ18707-13, QMJ18716-23, QMJ18725-26, QMJ18729, QMJ19824, QMJ23855-56, QMJ23952, QMJ27399-402, QMJ27449, QMJ27451, QMJ27453, QMJ27483, QMJ27949, QMJ29259, QMJ29263, QMJ29277-79, QMJ29990-91, QMJ30085, QMJ30878, QMJ30882, QMJ31881, QMJ31886-89, QMJ32209, QMJ34160-61, QMJ35108, QMJ35801-06, QMJ36902, QMJ37032-33, QMJ37470, QMJ37543, QMJ39268, QMJ40141-49, QMJ40176, QMJ40214-15, QMJ40258, QMJ40442-46, QMJ40517-19, QMJ41959, QMJ42158-59, QMJ42186, QMJ42220, QMJ42643-69, QMJ42671, QMJ42677, QMJ42691, QMJ42749, QMJ42751-53, QMJ42757, QMJ42760-64, QMJ43850-51, QMJ49439, QMJ50630, QMJ50632, QMJ50637-42, QMJ50644-56, QMJ52285, QMJ54402-05, QMJ55019, QMJ55021, QMJ55194, QMJ56789, QMJ57286, QMJ58434. Data as for type description.

Rheobatrachus vitellinus

Mahony, Tyler & Davies, 1984

Holotype QMJ42529; paratype QMJ42145. Data as for type description.

Taudactylus pleione

Czechura, 1986

Holotype QMJ42392; paratypes QMJ42137, QMJ42388-91, QMJ42422-23. Data as for type description.

Uperoleia altissima

Davies, Watson, McDonald, Trenerry & Werren, 1993

Holotype QMJ55301; paratypes QMJ19851-52, QMJ19855-587, QMJ51780-84. Data as for type description.

Uperoleia capitulata

Davies, McDonald & Corben, 1986

Holotype QMJ26428; paratypes QMJ26416, QMJ26427, QMJ39196, QMJ45956-60. Data as for type description.

Uperoleia fusca

Davies, McDonald & Corben, 1986

Paratypes QMJ10900-02, QMJ12294, QMJ12309, QMJ12323, QMJ12721, QMJ18817, QMJ18822, QMJ18825, QMJ18832, QMJ18837, QMJ19925, QMJ19927, QMJ19930, QMJ19936, QMJ19938-39, QMJ19941-43, QMJ19947, QMJ19952-53, QMJ19956-59, QMJ19961, QMJ19965-66, QMJ24088, QMJ27475, QMJ27477, QMJ27481, QMJ27563, QMJ27905, QMJ29280, QMJ30606, QMJ31556-62, QMJ31582, QMJ39315, QMJ40020, QMJ40315, QMJ40431, QMJ40433-35, QMJ40484, QMJ40486-87, QMJ40489-90, QMJ41533, QMJ42563-76, QMJ42578-614, QMJ45961-65. Data as for type description.

Uperoleia littlejohni

Davies, McDonald & Corben, 1986

Holotype QMJ45949; paratypes QMJ29874, QMJ38877-80, QMJ38883, QMJ38915, QMJ43154-55, QMJ45950-54. Data as for type description. After providing a list of paratypes (p. 175), the authors list cleared and stained paratypes separately (p. 178). Here they fail to mention QMJ45952 and QMJ45954, both cleared and stained specimens already listed on p. 175. Further, QMJ35427 is erroneously listed as a cleared and stained paratype. This number is for a specimen of *Ctenotus robustus*.

Uperoleia mimula

Davies, McDonald & Corben, 1986

Holotype QMJ45943; paratypes QMJ19859, QMJ38271-72, QMJ40234-35, QMJ40247, QMJ42534-35, QMJ42537, QMJ45944-48. Data as for type description.

Class REPTILIA

Family CHELIDAE

Elusor macrurus

Cann & Legler, 1994

Holotype QMJ51275; paratypes QMJ51274, QMJ51468-70, QMJ54138-40. Data as for type description.

Rheodytes leukops

Legler & Cann, 1980

Holotype QMJ31701; paratypes QMJ31702-7. Data as for type description.

Family GEKKONIDAE

Bavayia septuiclavus

Sadlier, 1988

Paratypes QMJ43985, QMJ44034. Data as for type description. Erroneously, QMJ44985 was listed in the type description instead of QMJ43985. The number QMJ44985 is for a specimen of *Morelia spilota*.

Bavayia validiclavus

Sadlier, 1988

Paratype QMJ43980. Data as for type description.

Nephrurus amya

Couper (in Couper & Gregson, 1994)

Paratypes QMJ51650, QMJ53650. Data as for type description.

Nephrurus sheai

Couper (in Couper & Gregson, 1994)

Paratypes QMJ52872, QMJ57515. Data as for type description.

Phyllurus isis

Couper, Covacevich & Moritz, 1993

Holotype QMJ53511; paratypes QMJ53480, QMJ53485-86, QMJ53512, QMJ53518, QMJ53591, QMJ53602-3. Data as for type description.

Phyllurus nepthys

Couper, Covacevich & Moritz, 1993

Holotype QMJ34058; paratypes QMJ32634-35, QMJ32669, QMJ32674-76, QMJ32695-96, QMJ32733, QMJ32740, QMJ34024-25, QMJ34076-79, QMJ35128, QMJ50992-93, QMJ51098-101, QMJ53330-32, QMJ53359-62. Specimen QMJ25411 is also a paratype of *Phyllurus caudiannulatus* Covacevich, 1975. Data as for type description.

Phyllurus ossa

Couper, Covacevich & Moritz, 1993

Holotype QMJ53444; paratypes QMJ53389-93, QMJ53414, QMJ53426-28, QMJ53443, QMJ53445-47, QMJ53507, QMJ56311, QMJ56766-75, QMJ56791-92. Data as for type description.

Saltuarius occultus

Couper, Covacevich & Moritz, 1993

Holotype QMJ37040; paratypes QMJ37037-39. Data as for type description.

Family PYGOPODIDAE

Delma labialis

Shea, 1987

Holotype QMJ45563; paratype QMJ30265. Data as for type description.

Delma mitella

Shea, 1987

Holotype QMJ32597. Data as for type description.

Family AGAMIDAE

Pogona brevis

Witten, 1994

Holotype QMJ32292; paratypes QMJ38735, QMJ38760-1, QMJ46949. Data as for type description.

Family SCINCIDAE

Anomalopus brevicollis

Greer & Cogger, 1985

Holotype QMJ42616; paratypes QMJ4561, QMJ33863, QMJ33870, QMJ34056, QMJ38740, QMJ41997-98, QMJ42454, QMJ46272. Data as for type description.

Anomalopus gowi

Greer & Cogger, 1985

Holotype QMJ42615; paratypes QMJ27617, QMJ31050. Data as for type description.

Anomalopus mackayi

Greer & Cogger, 1985

Paratypes QMJ8516, QMJ42433, QMJ42531. Data as for type description.

Anomalopus swansoni

Greer & Cogger, 1985

Paratype QMJ44236. Data as for type description.

Calypotis lepidorostrum

Greer, 1983

Holotype QMJ33612; paratypes QMJ22067, QMJ22274, QMJ22472-73, QMJ23810, QMJ24133, QMJ24373, QMJ25397, QMJ29093, QMJ30229, QMJ30231, QMJ30236, QMJ31575, QMJ32653-55, QMJ32671, QMJ32673, QMJ32707-16, QMJ32721-22, QMJ32734-38, QMJ33610, QMJ33613-15, QMJ33737, QMJ33752, QMJ35309, QMJ35878-82, QMJ50545-48. Data as for type description.

Calypotis ruficauda

Greer, 1983

Paratype QMJ26024. Data as for type description.

Calypotis temporalis

Greer, 1983

Holotype QMJ32594; paratypes QMJ13718, QMJ25742-43, QMJ34089, QMJ35088. Data as for type description.

Calypotis thornstonensis

Greer, 1983

Holotype QMJ28354. Data as for type description.

Carlia parrhasius

Couper, Covacevich & Lethbridge, 1994

Holotype QMJ57868; paratypes QMJ57867, QMJ57869. Data as for type description.

Carlia pectoralis inconnexa

Ingram & Covacevich, 1989

Paratypes QMJ25060, QMJ42496. Data as for type description.

Carlia rubrigularis

Ingram & Covacevich, 1989

Holotype QMJ29956; paratypes QMJ17826, QMJ17901, QMJ17906-07, QMJ22668, QMJ24649, QMJ24800, QMJ24807-08, QMJ25141, QMJ25143, QMJ25146, QMJ25198-200, QMJ25209, QMJ25211-12, QMJ25240, QMJ25242, QMJ25245-50, QMJ25272, QMJ25293-94, QMJ25296-97, QMJ50335. Specimen QMJ25229 was listed as a paratype (Ingram & Covacevich, 1989). This specimen has now been re-registered as QMJ50335. The number QMJ25229 had been assigned also to a paratype of *Lampropholis basiliscus*. Data as for type description.

Carlia storri

Ingram & Covacevich, 1989

Holotype QMJ24656; paratypes QMJ17804, QMJ17895-96, QMJ17908, QMJ24639-40, QMJ24653-55, QMJ24657-58, QMJ24676, QMJ24683-85, QMJ24691, QMJ25312, QMJ25429, QMJ25600, QMJ26222, QMJ26256, QMJ26269. Data as for type description.

Ctenotus allotropis

Storr, 1981

Paratypes QMJ31847-8, QMJ34770. Data as for type description.

Ctenotus aphrodite

Ingram & Czechura, 1990

Holotype QMJ41814. Data as for type description.

Ctenotus arcanus

Czechura & Wombey, 1982

Holotype QMJ36925; paratypes QMJ437-38, QMJ440-42, QMJ1682, QMJ11030, QMJ12111-12, QMJ30266, QMJ30722-23, QMJ31863, QMJ34588, QMJ38695. Data as for type description.

Ctenotus astarte

Czechura, 1986

Holotype QMJ26499; Paratypes QMJ39580, QMJ40182-83, QMJ41603, QMJ41796. Data as for type description

Ctenotus capricorni

Storr, 1981

Holotype QMJ39470. Data as for type description. This specimen is listed in the type description as AM R65946.

Ctenotus essingtonii brevipes

Storr, 1981

Holotype QMJ39469. Data as for type description.

Ctenotus eurydice

Czechura & Wombey, 1982

Paratypes QMJ1618, QMJ15614, QMJ27526, QMJ39223. Data as for type description.

Ctenotus eutaenius

Storr, 1981

Holotype QMJ39467. Data as for type description. This specimen is listed as AM R93408 in type description.

Ctenotus hypatia

Ingram & Czechura, 1990

Holotype QMJ42092. Data as for type description.

Ctenotus ingrami

Czechura & Wombey, 1982

Holotype QMJ34792; Paratype QMJ34791. Data as for type description.

Ctenotus monticola

Storr, 1981

Holotype QMJ39468. Data as for type description. This specimen is listed in the type description as AMR70937.

Ctenotus nullum

Ingram & Czechura, 1990

Holotype QMJ32424; paratypes QMJ24647, QMJ24705, QMJ37999-38001, QMJ41023-25, QMJ42736, QMJ42768-69. Data as for type description.

Ctenotus serotinus
Czechura, 1986

Holotype QMJ43313; paratype QMJ40185. Data as for type description.

Ctenotus terrareginae
Ingram & Czechura, 1990

Holotype QMJ41996. Data as for type description.

Ctenotus zebrilla
Storr, 1981

Holotype QMJ39471. Data as for type description. This specimen is listed in the type description as AMR63316.

Emoia atrocostata australis
Brown, 1991

Paratype QMJ24732. Data as for type description.

Eulamprus frerei
Greer, 1992

Holotype QMJ47985; paratype QMJ39531. Data as for type description.

Eulamprus sokosoma
Greer, 1992

Holotype QMJ27702; paratypes QMJ15668, QMJ25915, QMJ27622-23, QMJ33843, QMJ34209, QMJ42506, QMJ42513, QMJ42516-17, QMJ42526, QMJ55403, QMJ55404. Data as for type description. Specimens QMJ55403 and QMJ55404 are listed in the type description as QNPWSN1787 and QNPWSN36821 respectively.

Lampropholis adonis
Ingram, 1991

Holotype QMJ35097; paratypes QMJ23805-08, QMJ23867, QMJ27725, QMJ27732, QMJ27820, QMJ27822, QMJ27825, QMJ27833, QMJ32644, QMJ32652, QMJ32701, QMJ32706, QMJ32754, QMJ32793, QMJ32795, QMJ33604, QMJ33607, QMJ33609, QMJ33701, QMJ33717-18, QMJ33720-24, QMJ33736, QMJ35104, QMJ35122, QMJ35198, QMJ45297-98, QMJ46191, QMJ49563, QMJ49573, QMJ49591, QMJ49597, QMJ49746-48, QMJ49750-51, QMJ49753, QMJ51319, QMJ51323. Data as for type description.

Lampropholis amicula
Ingram & Rawlinson, 1981

Holotype QMJ24333; paratypes QMJ22729, QMJ24330-2, QMJ24496-7, QMJ27523, QMJ30828, QMJ31308, QMJ32090, QMJ32519, QMJ37177-78, QMJ37288-89. Data as for type description. Erroneously, QMJ34330-31 were listed in the type description instead of QMJ24330-31. Numbers QMJ34330-31 are for specimens of *Lechriodus fletcheri*. One of the paratypes, QMJ37287 has been transferred to the Australian Museum's herpetological collection, with the registration number AMR96587.

Lampropholis basiliscus
Ingram & Rawlinson, 1981

= *Saproscincus basiliscus* after Greer (1989).

Holotype QMJ34409; paratypes QMJ11161, QMJ12145-47, QMJ12158-59, QMJ17435, QMJ17902-03, QMJ24648, QMJ24848, QMJ24918, QMJ25022-27, QMJ25029-45, QMJ25047-59, QMJ25061, QMJ25137-38, QMJ25204, QMJ25229, QMJ25257, QMJ25265, QMJ25289, QMJ25301, QMJ25308, QMJ25450, QMJ25825-75, QMJ26330-32, QMJ26375-76, QMJ27135, QMJ27141, QMJ27258, QMJ29668, QMJ30810-11, QMJ32354, QMJ32602, QMJ32605, QMJ32758, QMJ32760, QMJ32766-71, QMJ32780-83, QMJ32794, QMJ34000-06, QMJ34036, QMJ34038-40, QMJ34042, QMJ34047, QMJ34062, QMJ34066, QMJ34069, QMJ34092-93, QMJ34095-100, QMJ34408. Data as for type description. Sadlier et al. (1993) treated *S. basiliscus* as a junior synonym of *S. spectabilis*. Following discussion of the type status of *Mococa spectabilis*, Ingram (1994) showed that *S. spectabilis* was a senior synonym of *S. galli* and not of *S. basiliscus* as proposed by Sadlier et al. (1993).

Lampropholis caligula
Ingram & Rawlinson, 1981

Paratype QMJ38704. Data as for type description.

Lampropholis coggeri
Ingram, 1991

Holotype QMJ27133; paratypes QMJ12205, QMJ14009, QMJ14022, QMJ14092, QMJ18006, QMJ21408, QMJ25139, QMJ25201-03, QMJ25217, QMJ25230, QMJ25241, QMJ25243-44, QMJ25251-55, QMJ25271, QMJ25285, QMJ25299, QMJ25300, QMJ25330, QMJ26301, QMJ27008-11, QMJ27130-32, QMJ27134, QMJ29622, QMJ39858, QMJ39864, QMJ39872, QMJ40536, QMJ40663, QMJ41733, QMJ42276-77, QMJ42294, QMJ48170, QMJ48172, QMJ48210. Data as for type description.

Lampropholis colossus

Ingram, 1991

Holotype QMJ49687; paratypes QMJ27549, QMJ27550, QMJ30655, QMJ30656, QMJ30657, QMJ30659-60, QMJ46095-97, QMJ49689, QMJ49692. Data as for type description.

Lampropholis couperi

Ingram, 1991

Holotype QMJ49575; paratypes QMJ25741, QMJ25745, QMJ27723, QMJ30293, QMJ30827, QMJ33605, QMJ34162, QMJ40153-57, QMJ42156, QMJ42426, QMJ43956, QMJ47950-51, QMJ49660, QMJ49669, QMJ49752, QMJ51663. Data as for type description.

Lampropholis czechurai

Ingram & Rawlinson, 1981

= *Saproscincus czechurai* after Greer (1989).

Holotype QMJ34402; paratypes QMJ12148-50, QMJ25227, QMJ27072-73, QMJ31201, QMJ31204-06, QMJ34403, QMJ34405-07. Data as for type description.

Lampropholis mirabilis

Ingram & Rawlinson, 1981

Holotype QMJ24439; paratypes QMJ4404, QMJ24339-40, QMJ24416, QMJ24424, QMJ24435, QMJ24437-38, QMJ24440-41, QMJ24528, QMJ27615, QMJ32555. Data as for type description.

Lampropholis robertsi

Ingram, 1991

Holotype QMJ43911; paratypes QMJ31194-200, QMJ39490-91, QMJ39855-57, QMJ40033, QMJ40036-39, QMJ40041, QMJ40609-10, QMJ41706-08, QMJ43912, QMJ43918, QMJ43958, QMJ43964, QMJ46193, QMJ47097, QMJ47956, QMJ47959, QMJ48295, QMJ49648, QMJ49659, QMJ51405-06, QMJ51948. Data as for type description.

Leiolopisma jigurru

Covacevich, 1984

= *Bartleia jigurru* after Hutchinson et al., (1990).

Holotype QMJ40040, paratypes QMJ39492-99. Data as for type description.

Leiolopisma zia

Ingram & Ehmann, 1981

= *Cautula zia* after Hutchinson et al., (1990).

Holotype QMJ30563; paratypes QMJ26025, QMJ27787-88, QMJ27793, QMJ27855-58, QMJ30213, QMJ30555-62. Data as for type description.

Lerista aericeps aericeps

Storr, 1986

Paratypes QMJ26502, QMJ34137, QMJ39572. Data as for type description.

Lerista cinerea

Greer, McDonald & Lawrie, 1983

Holotype QMJ40097; paratypes QMJ40094-96, QMJ40098-100. Data as for type description.

Lerista colliveri

Couper & Ingram, 1992

Holotype QMJ16181; paratypes QMJ16182-83, QMJ33123-28, QMJ45648, QMJ46266-67. Data as for type description.

Lerista emmotti

Ingram, Couper & Donnellan, 1993

Holotype QMJ53959; paratypes QMJ9038, QMJ50066, QMJ50068-69, QMJ51217-18, QMJ51529, QMJ51629-30, QMJ52585-87, QMJ53958, QMJ53960, QMJ54144-46, QMJ54292, QMJ54491-93. Data as for type description.

Lerista ingrami

Storr, 1991

Holotype QMJ32396; paratypes QMJ20644-51, QMJ20653. Data as for type description.

Lerista storri

Greer, McDonald & Lawrie, 1983

Holotype QMJ39480; paratype QMJ39481. Data as for type description.

Lerista vittata

Greer, McDonald & Lawrie, 1983

Holotype QMJ40102; paratypes QMJ40101, QMJ40103-04. Data as for type description.

Lerista zonulata

Storr, 1991

Holotype QMJ54137; paratypes QMJ31223, QMJ38756, QMJ46268, QMJ47103. Data as for type description. The holotype is listed in the type description as AMR63747.

Lygisaurus rococo

Ingram & Covacevich, 1988

Holotype QMJ46014; paratype QMJ42068. Data as for type description.

Lygisaurus sesbrauna

Ingram & Covacevich, 1988

Holotype QMJ24664; paratypes QMJ24620, QMJ24630-32, QMJ25599, QMJ25602, QMJ25615, QMJ25990, QMJ25993, QMJ26204-06, QMJ26236, QMJ26259, QMJ28057, QMJ32512, QMJ32516, QMJ34461-63, QMJ34465, QMJ34578, QMJ37508, QMJ37510, QMJ37513-20, QMJ37522-26, QMJ37530-31, QMJ38092, QMJ38299, QMJ42113. Data as for type description.

Lygisaurus tanneri

Ingram & Covacevich, 1988

Holotype QMJ32352; paratypes QMJ20609-11, QMJ22380, QMJ22789, QMJ24117-18, QMJ27093-96, QMJ32358-59, QMJ32362-64, QMJ42771-72. Data as for type description.

Lygisaurus zuma

Couper, 1993

Holotype QMJ55760; paratypes QMJ53397, QMJ55761-67, QMJ56278-80, QMJ56765, QMJ56786, QMJ56874-76, QMJ56883. Data as for type description.

Menetia koshlandae

Greer, 1991

Holotype QMJ50554; paratype QMJ45800. Data as for type description.

Menetia sadlieri

Greer, 1991

Holotype QMJ24448. Data as for type description. This specimen is also a paratype of *Menetia timlowi* Ingram, 1977.

Nangura spinosa

Covacevich, Couper & James, 1993

Holotype QMJ55424; paratypes QMJ56029, QMJ56031, QMJ57246-47. Data as for type description.

Ophioscincus cooloolensis

Greer & Cogger, 1985

Holotype QMJ31573; paratypes QMJ27381-85, QMJ31574, QMJ31578, QMJ40092, QMJ40223-26. Data as for type description.

Sphenomorphus cracens

Greer, 1985

= *Glaphyromorphus cracens* after Greer (1989).

Holotype QMJ42714; paratypes QMJ1535-36, QMJ31022, QMJ31029-31, QMJ31043-49, QMJ42070-74, QMJ46261-65. Data as for type description.

Family VARANIDAE

Odatia keithhornei

Wells & Wellington, 1985

= *Varanus keithhornei* - new synonymy

Holotype QMJ31566. Data as for type description. This specimen is also the holotype of *Varanus teriae* Sprackland, 1991.

Varanus telenesetes

Sprackland, 1991

Holotype QMJ1190. Data as for type description.

Varanus teriae

Sprackland, 1991

= *Varanus keithhornei* (Wells & Wellington, 1985).

Holotype QMJ31566; paratypes QMJ35450-51. Data as for type description. This specimen is also the holotype of *Odatia keithhornei* Wells & Wellington, 1985.

Family TYPHLOPIDAE

Ramphotyphlops chamodracaena

Ingram & Covacevich, 1993

Holotype QMJ40233; paratypes QMJ28082, QMJ31963, QMJ39673, QMJ41550, QMJ51980. Data as for type description.

Ramphotyphlops silvia
Ingram & Covacevich, 1993

Holotype QMJ27387; paratypes QMJ8521, QMJ23620, QMJ27386, QMJ31576-77, QMJ31579, QMJ35872, QMJ43785, QMJ46128. Data as for type description.

Family BOIDAE

Liasis stimsoni orientalis
Smith, 1985

= *Antaresia stimsoni* after Kluge (1993).

Paratypes QMJ390, QMJ5963, QMJ7154, QMJ10256-58, QMJ10274, QMJ10444, QMJ28432, QMJ29032, QMJ32284-85, QMJ35685, QMJ39087. Data as for type description.

NEW INFORMATION ON SPECIES
INCLUDED IN PREVIOUS QUEENSLAND
MUSEUM TYPE LISTS

Class AMPHIBIA
Family MYOBATRACHIDAE

Mixophyes balbus
Straughan, 1968

Thirteen specimens of this species are listed as in the Australian and the Queensland Museums (Straughan, 1968). Covacevich (1971) noted that the Straughan collection held in the Queensland Museum contained '*M. balbus* - 10 unsexed specimens, unregistered, found with tadpoles in jar labelled New England sp. nov. *M. balbus*, but with no other data.' Cogger (1979) listed six *M. balbus* paratypes in the Australian Museum. Assuming they are paratypes, there should be only seven paratypes in the Queensland Museum. Corben & Ingram (1987) examined the ten specimens referred to by Covacevich (1971) and noted 'these specimens are now registered as QMJ45785-45794. We have examined them and found that three (QMJ45785-7) are *M. fasciolatus* and the other seven (QMJ45788-94) are *M. balbus*.' These seven specimens are probably the missing seven paratypes, and are labelled so in the collection.

Mixophyes iteratus
Straughan, 1968

Two paratypes were apparently lodged in the Queensland Museum from Tweed River, Mount Warning, NSW (Straughan, 1968). Covacevich (1971) noted the Straughan collection in the Queensland Museum contained '*M. iteratus* - 2 unsexed specimens, QMJ18851, Lynch's Creek, Kyogle, N.S.W.; 1 unregistered specimen

without data.' Corben & Ingram (1987) noted 'QMJ18851 from Lynch's Creek, Kyogle' did not agree with the given locality of 'Tweed River, Mount Warning. The other specimen (now registered as QMJ45796) had no accompanying data.' The status of these two specimens thus remains uncertain.

Class REPTILIA
Family GEKKONIDAE

Gehyra catenata
Low, 1979

Ingram & Covacevich (1981) erroneously listed QMJ28794 as a paratype. This number is for a specimen of *Gehyra dubia*.

Oedura cincta
de Vis, 1888

= *Oedura marmorata* Gray, 1842 after Cogger (1957).

Specimen QMJ226 was listed by Covacevich (1971) as a '? syntype'. Wells & Wellington (1985) have designated this specimen as the lectotype.

Phyllurus caudiannulatus
Covacevich, 1975

Paratype QMJ25411. This specimen is also a paratype of *P. nephyss* Couper, Covacevich & Moritz, 1993.

Family SCINCIDAE

Ablepharus boutonii clarus
Storr, 1961

= *Cryptoblepharus virgatus* Garman, 1901 after Cogger et al. (1983).

Paratypes QMJ30920-21. The type description alludes to 'cotypes' and 'paratypes', without registration numbers. Close to thirty years after his description, Storr identified these specimens as paratypes (Storr, in litt., 23 March 1990).

Heteropus bicarinatus
Macleay, 1877

= *Carlia bicarinata* after Ingram & Covacevich (1989).

Neotype QMJ27717, designated by Ingram & Covacevich (1989).

Heteropus blackmanni
de Vis, 1884

= *Carlia vivax* (de Vis, 1884) after Ingram & Covacevich (1989).

Lectotype QMJ19985; paralectotypes QMJ7773?, QMJ19968-84, QMJ19986-90

Lectotype designated by Ingram & Covacevich (1989). In their discussion of the status of material associated with the type specimen history of *Carlia vivax*, they refer to QMJ19986-90 twice. The second reference is erroneous, as QMJ19986-99. See Covacevich (1971) for detail of doubtful type status of QMJ7773.

Heteropus lateralis
de Vis, 1884

= *Carlia pectoralis pectoralis* (de Vis, 1884) after Ingram & Covacevich (1989).

Lectotype QMJ234, designated by Ingram & Covacevich (1989).

Heteropus mundus
de Vis, 1884

= *Carlia munda* after Ingram & Covacevich (1989).

Neotype QMJ15654, designated by Ingram & Covacevich (1989).

Lygisaurus foliorum
de Vis, 1884

Neotype QMJ23660, designated by Ingram & Covacevich (1988).

Menetia timlowi
Ingram, 1977

Paratype QMJ24448. This specimen is also the holotype of *Menetia sadlieri* Greer, 1991.

Mocoa delicata
de Vis, 1888

= *Lampropholis delicata* after Mather (1990).

Neotype QMJ45765, designated by Mather (1990).

Mocoa spectabilis
de Vis, 1888

= *Saproscincus spectabilis* after Wells & Wellington (1985).

The type status history of specimens of this taxon is complicated. Covacevich (1971) treated QMJ244, QMJ255, QMJ19742-3 as syntypes, while noting that measurements of QMJ244 fitted those in the type description. Wells & Wellington (1985) designated QMJ19742 as the lectotype. Specimens QMJ244,

QMJ255 and QMJ19743 thus became paralectotypes. Sadlier et al. (1993) recognised the work of Wells & Wellington (1985), and recommended nomenclatural changes based on it. Ingram (1994), asserted Covacevich's (1971) recognition of four syntypes was erroneous and that the type description (de Vis, 1888) was based on one specimen only, the holotype, QMJ244. His action thus overturned the nomenclatural change recommended by Sadlier et al. (1993).

Myophila vivax
de Vis, 1884

= *Carlia vivax* after Ingram & Covacevich (1989).

Neotype QMJ24176, designated by Ingram & Covacevich, 1989.

Rhodona allanae
Longman, 1937

= *Lerista allanae* after Greer (1976).

The holotype of this species, '... Described from three specimens ...', was designated (QMJ6180) by its author (Longman, 1937). However, registration numbers for the two paratypes were not listed. The question of which specimens are the paratypes has already been addressed twice, with different opinions.

Covacevich (1971) found three specimens in jars with a tag marked '*Rhodona allanae* Lgmn. Paratypes'. This tag has been checked, and is in Longman's handwriting (I. Filmer, pers. comm.). The three specimens are QMJ6040, QMJ6238 and QMJ6308. The last mentioned is incomplete, lacking head and some body. Assuming Longman would have mentioned a damaged specimen in his description if it were part of his type series, yet acknowledging the possibility that it may have been a type as the Longman handwritten tag suggested, she listed QMJ6040 and QMJ6238 as paratypes and QMJ6308 as a '? paratype', signifying 'possible type status'. Erroneously, she did not mention QMJ6179, stored separately from the former three specimens, but identified in the register 'paratype', also in Longman's handwriting.

Couper & Ingram (1992) commented on this decision '... there is no doubt about QMJ6040, both the dates of registration of QMJ6238 and QMJ6308 (28 June, 1937 and 30 November, 1937 respectively) are after the date of publication of Longman's paper (24 June, 1937) and thus unlikely to have been examined for the paper. Actually the second paratype must be QMJ6179, which was registered with the holotype and is noted as 'paratype' in the register.'

Data for these specimens from the register and from the tag found by Covacevich (1971), all in Longman's hand are:

| Reg. number and Date | Labelled 'paratype'? | | Locality/donor/other relevant data |
|---------------------------|-------------------------|----------|--|
| | Jar | Register | |
| QMJ6040 15 Sept., 1936 | yes | yes | Retro Station, Capella, Q.; Mrs P.C. Allan |
| QMJ6179 19 May, 1937 | yes | - | Retro Station, Capella, Qld; Mrs P.C. Allan |
| QMJ6238 28 June, 1937 | yes | - | Retro, Capella, Q; Mrs P.C. Allan; 'on exhibition' |
| QMJ6308 30 Nov., 1937 | yes | - | Retro, Capella, Qld; Mrs P.C. Allan; '1/2 body only' |

Dates of publication which appear on journals are not invariably their true dates of publication; many type specimens have been registered after their descriptions have been published, a situation easily possible where registration numbers are not published (as is the case here); and the registration date of QMJ6179 (19 May, 1937) is less than five weeks earlier than the date of publication which appears on the type description (24 June, 1937). As a five week turn around time between submission of manuscript and publication of a journal is extremely rapid by even present highly mechanised standards, it seems reasonable to suggest that this specimen must have been registered by Longman after his paper had gone to press. Further, the registration date of QMJ6238 is only four days after the alleged date of publication of the paper (28 June, 1937 vs 24 June, 1937).

Article 72 B vii of the International Code of Zoological Nomenclature (3 ed., 1985) states 'The mere citation of "Type" or equivalent expression, in a list of types, or in a catalogue in a museum, or on a label is not to be construed alone as evidence that a specimen is or is fixed as any of the kinds of types...' (italics ours). Recommendation 72 B states 'External evidence admitted. - If an author, in establishing a nominal species-group taxon, does not explicitly state what specimens constitute the type series, evidence in addition to published evidence may be taken into account (e.g., labels by the original author and specimens known to have been in appropriate collections at the appropriate time).' ...

If dates of publication and registration are considered along with type designation by Longman either in the register or in a jar, three specimens are possible candidates for status as two paratypes. (Specimen QMJ6308 can be excluded from further consideration because of a late date of registration and as an incomplete specimen, despite its presence with the Longman paratype label). Of the three candidates for type status (QMJ6040, QMJ6179, QMJ6238), it seems reasonable to exclude QMJ6238 as a possible paratype because, according to the register it was

'on exhibition' (Longman's handwriting). This specimen, once removed from exhibition, could easily have been placed in the jar containing QMJ6040 and QMJ6179, the paratypes, along with Longman's original paratype label. We thus confirm the correction by Couper & Ingram (1992) of Covacevich's (1971) decision, but for reasons which differ from theirs.

Family ELAPIDAE

Denisonia rostralis

de Vis, 1911

= *Simoselaps warro* (de Vis, 1911) after Mack & Gunn (1953).

Holotype QMJ193. The holotype was not located by Covacevich (1971) and was listed 'presumed lost' by Cogger et. al. (1983) but has been discovered in the Queensland Museum collection.

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NEW PHASCOGALE TAPOATAFA (BRUSH-TAILED PHASCOGALE) RECORDS FROM CAPE YORK PENINSULA, AUSTRALIA. *Memoirs of the Queensland Museum* 37(1):82, 1994:- *Phascogale tapoatafa* is a species rarely seen, and sometimes difficult to find, even by spotlighting and trapping (Traill & Coates, 1993). Recent work (Sharpe, 1993) has shown that '... in prime habitat, one individual every 35ha is the norm. ... It is widely, but patchily, distributed in coastal areas of Australia with an average annual rainfall of between 500 and 2000mm (Cuttle, 1982; Cuttle in Strahan, 1983). In Queensland, it is well known in the southeast, but specimens or reliable sightings of *P. tapoatafa* in other parts of the state are scant. There are records from the central coastal area (Rockhampton, 23°22'S 150°32'E; Ingram & Raven, 1991); and from northern Cape York Peninsula (Coen, 13°52'S 143°12'E; Lockhart R. area 13°04'S 143°24'E; Cuttle, 1982; Dixon & Huxley, 1985); and from skeletal remains in limestone caves at Chillagoe, on southeastern Cape York Peninsula, 17°09'S 144°31'E; Tresize, 1970. There is also one doubtful record from the western coast of Cape York Peninsula (Edward R. 14°39'S 142°03'E; D. Thomson, 1929, p.29 in Dixon & Huxley, 1985). This apparent sight record conflicts with data in the same reference (p.14): '... *Phascogale tapoatafa* ... not uncommon in places on east coast; not seen on western fall of central range. ...

Some recent specimen and sight records shed light on the occurrence of this elusive species on Cape York Peninsula:

Nr McLeod Ck, McIvor R. Rd, 14°16'S 144°27'E, killed by cat, specimen not retained, 1 Sept 1976, L. Kuhneman; Iron Ra., 12°43'S 143°17'E, Jun 1978, G. Czechura, sight only; Mt. Molloy, 2.5km N of Rifle Ck, 16°40'S 145°20'E, 1 Aug 1986, L. Moore & F. Crome, sight only; Emerald Ck on Cairns-Mareeba Rd, 16°58'S 145°28'E, 17 Jun 1992, J. Grant, sight only; Lamb Ra., Emu Ck Rd, 17°03'S 145°28'E, 5 Aug 1993, D.L. Storch, sight only; Lamb Ra., Emu Ck Rd 17°04'S 145°30'E, 5 Aug 1993, D.L. Storch & N. Goudberg, sight only; QMJM10591, dead on road, 20km W of Cooktown on McIvor R. Rd, 15°26'S 145°03'E, Nov 1993, L. Roberts; QMJM10579 dead on road, 8km S of McIvor R., McIvor Rd 15°20'S 145°04'E, 13 Jun 1994, J. Covacevich, L. Roberts; Eubardt Pt, Lockhart R., 12°58'S 143°30'E, no date recorded, W. Butcher, in Leung et al., 1994.

One of the two McIvor Rd specimens (QMJM10591) was found on a road which runs between a narrow band of riverine

rainforest and open woodland. The second (QMJM10579) was found dead on that road in sparse open woodland. Both Lamb Ra. observations were made in open forests on soils derived from granite. Ground cover is sparse in the area. Data on vegetation are not available for other localities at which specimens have been collected or observed.

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A NEW SPECIES AND A NEW RECORD OF *HEPATOPORUS* FROM NORTH-WESTERN AUSTRALIA (CRUSTACEA: DECAPODA: XANTHIDAE)

P.J.F. DAVIE AND P.A. TURNER

Davie, P.J.F. & Turner, P.A. 1994 12 01: A new species and a new record of *Hepatoporus* from northwestern Australia (Crustacea: Decapoda: Xanthidae). *Memoirs of the Queensland Museum* 37(1):83-86. Brisbane. ISSN 0079-8835.

Hepatoporus asper sp. nov., is described from the North-West Shelf, Western Australia. It is separated from other *Hepatoporus* by its carapace regions being separated by deep channels lined with mushroom shaped tubercles. *H. guinotae* (Zarenkov, 1971) is recorded for the first time from Australian waters, greatly extending its range from west Africa and the Red Sea. It is suggested that *H. distinctus* (Takeda & Nagai, 1986) is of uncertain validity and may prove to be a junior synonym of *H. guinotae*. □ Crustacea, Decapoda, Brachyura, Xanthidae, Euxanthinae, *Hepatoporus*, Australia, new species, distribution.

P.J.F. Davie & P.A. Turner, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 2 May 1994.

Two species of the xanthid *Hepatoporus* were identified in dredged material from the North-West Shelf, collected by the CSIRO aboard the R.V. 'Soela'. One, *H. guinotae* (Zarenkov, 1971) marks a considerable range extension and is a new record for Australia; the other is a new species, *H. asper*.

Hepatoporus was established by Serène (1984) to include *Carpoporoides orientalis* Sakai, 1935, from Japan, and *C. guinotae* Zarenkov, 1971, from the Red Sea and the western Indian Ocean. Sakai (1935) and Zarenkov (1971) had both noted that the closest relative to their species was *Carpoporoides papulosus* Stimpson, 1871, a West Atlantic species. Takeda & Nagai (1986) independently recognised the generic differences between *C. papulosus* and the two Indo-West Pacific species, and described the new genus *Carpoporoides* for them, as they did not know of the work of Serène (1984). Takeda & Nagai (1986) also described a new species, *Carpoporoides distinctus*, from Koza, Japan. Later, Takeda (1986) recognised *Carpoporoides* as a junior synonym of *Hepatoporus*.

Hepatoporus now contains four species: *H. orientalis* (Sakai, 1935), *H. guinotae* (Zarenkov, 1971), *H. distinctus* (Takeda & Nagai, 1986) and *H. asper* sp. nov.

Measurements given in the text are of the carapace breadth (measured at the widest point) followed by length.

ABBREVIATIONS: G1, gonopod 1; QM, Queensland Museum, Brisbane; P1-P5, pereopods 1-5.

SYSTEMATICS

Family XANTHIDAE MacLeay, 1838
Sub-family EUXANTHINAE Alcock, 1898

Hepatoporus guinotae (Zarenkov, 1971)
(Fig. 1A, B)

Carpoporoides guinotae Zarenkov, 1971: 191, fig. 86.
Hepatoporus guinotae: Serène, 1984: 74, 75, fig. 40,
pl. 10, d-f; Takeda, 1986: 51.

MATERIAL EXAMINED

QMW15071, ♀ (8.3 x 6.3mm), R.V. 'Soela', Stn 01B18NT, 22.2.1983, 52m, 20°01.4'S, 116°57.3'E, North-West Shelf, Western Australia; QMW14778, ♂ (3.1 x 2.6mm), R.V. 'Soela', Stn 02B02S, 22.4.1983, 43m, 19°56.9'S, 117°53.7'E, North-West Shelf, Western Australia.

REMARKS

The hepatic cavities of the two specimens show different states of development which may be age rather than sex related. The small male has only weakly developed cavities that make only slight impressions on the anterolateral margins, whereas those of the larger female are close to the state seen in Serène's illustration of a male from Kenya (Serène 1984: pl. 10d,e,f). The posterior part of the hepatic cavity is not as deeply excavated posteriorly as in Serène's specimen, but is much more deeply excavated than on the holotype of *H. distinctus*. Since the depth and shape of the hepatic cavity is the only significant character separating *H. guinotae* and *H.*

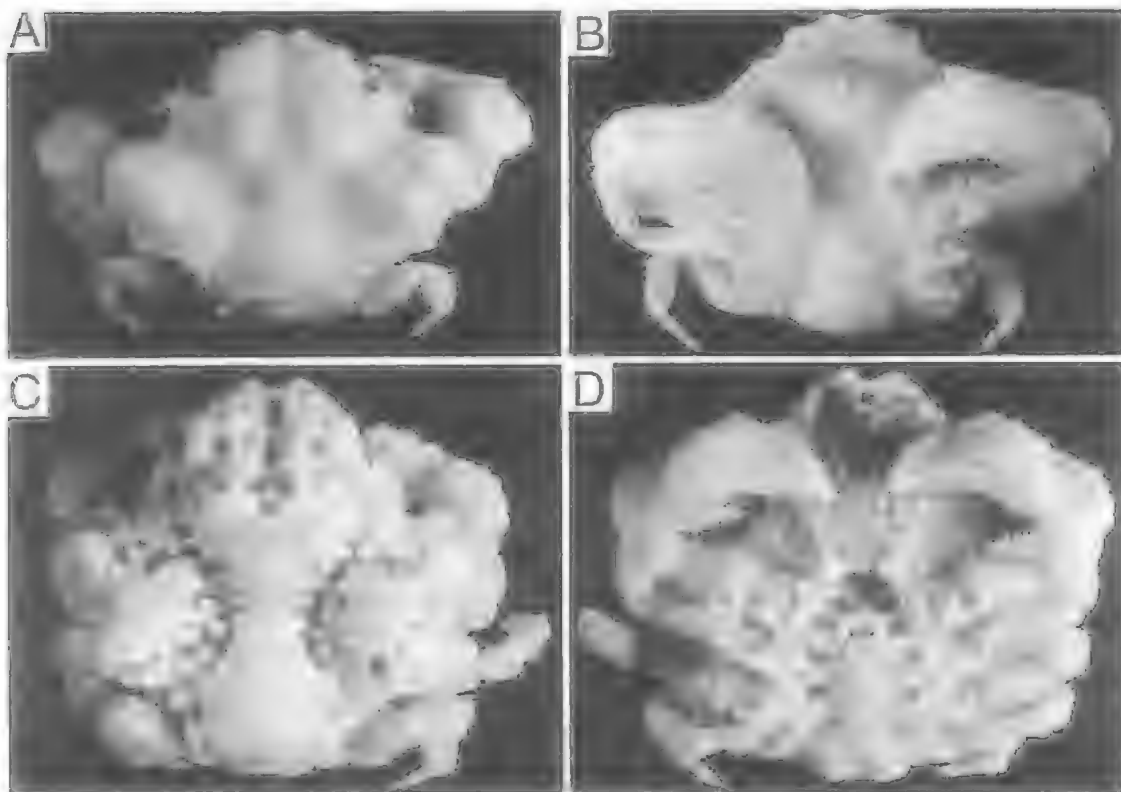


FIG. 1. A, B, *Hepatoporus guinotae* (Zarenkov), QMW15071, ♀ (8.3 x 6.3mm); C, D, *Hepatoporus asper* sp. nov., QMW19896, ♂ holotype (9.1 x 8.7mm).

distinctus Takeda & Nagai, 1986, we would be surprised if this later species proves to be validly separable; a greater range of material is needed to decide the matter.

DISTRIBUTION

Red Sea (type locality, Zarenkov, 1971); Madagascar, Kenyan Coast (Serène, 1984); and northwestern Australia. Bathymetric range: 108m (Serène, 1984) and 42-52m (this paper).

Hepatoporus asper sp. nov. (Figs 1C, D; 2A, B)

MATERIAL EXAMINED

HOLOTYPE: QMW19896, ♂ (9.1 x 8.7 mm), R.V. 'Soela', Stn 05B03BT, 26.10.1983, 40m, 19°55'S, 117°56.0'E, North-West Shelf, Western Australia.

DESCRIPTION

Carapace. Carapace heptagonal in outline, length 0.97 × width. Dorsal surface formed by a pavement of abutting mushroom-shaped

tubercles, eroded in appearance, with prominent raised pair of sub-conical, sub-median gastric prominences and moderately inflated branchial regions. Cardiac region uniformly convex, smoother but less raised than branchials. Lateral margins with 2 marked concavities, anterior hepatic and lateral branchial; dorsal surface broadly excavated obliquely behind posterior cavity. Gastro-cardiac regions separated from branchials by deep sulci; sulci forked anteriorly around hepatic regions; sulci with marginal mushroom shaped tubercles. Deep median sulcus separating frontal lobes, extending posteriorly to between gastric prominences. Deep, often inter-connecting, pits on most regions. Intestinal region bears 7 small, obtuse teeth at its edge. Frontal width 0.37 × width of carapace; deflexed, pitted; bilobed, with inner projections forming basal circular hole. Postero-lateral margins concave.

Antennular fossae broad, oblique; basal segment of antennae deeply pitted; epistome and anterior pterogostomial region pitted; posterior

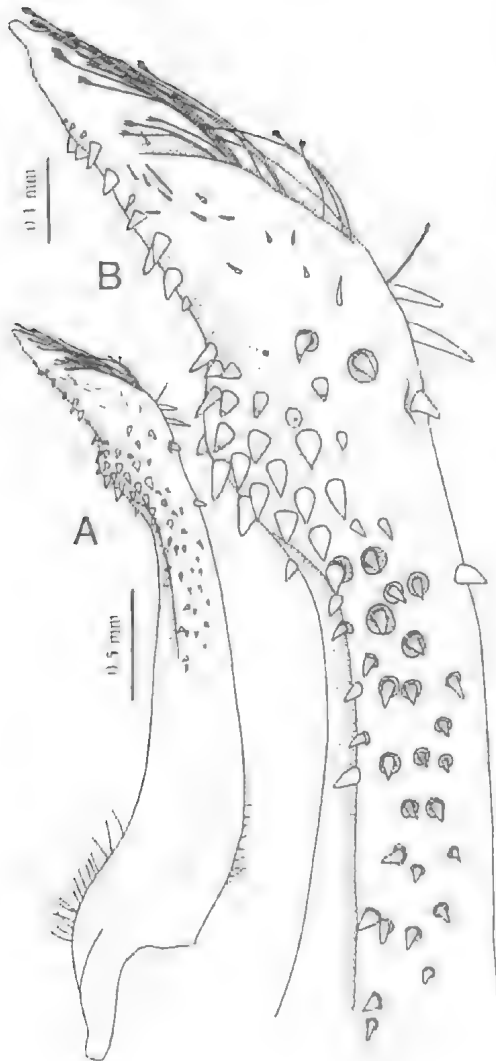


FIG. 2. First male gonopod of *Hepatoporus asper* sp. nov., holotype, QMW19896. A, abdominal view; B, enlarged view of apex.

half of pterogostomial and sub-hepatic regions coarsely granular.

Outer edge of orbit with several short, simple setae on inside edge; orbital margin relatively smooth, with few sparse, low, obtuse lobes.

Third maxillipeds. Surface coarsely pitted, some joining to form irregular longitudinal channels. Ischium c. $2 \times$ length of merus. Proximal half of exopod smooth, separated from pitted distal portion by smooth oblique ridge.

Thorax and abdomen. Thoracic sternites deeply eroded. Abdominal segments 3 - 5 fused, surface formed by pavement of abutting mushroom-shaped tubercles.

Chelipeds. Equal, short, length subequal carapace length. Fingers with tips crossing when closed. Upper surface of dactyl tuberculate proximally, becoming smooth distally. Outer surface of prodopos appearing coarsely granular, with more or less coalesced low, mushroom-like tubercles; ventral surface with small, smooth tubercles grading into smaller more sparsely dispersed granules on inner surface. Upper and outer surface of carpus similar to palm; inner and dorsal surface granular. Ventral surface of merus smooth; inner surface sparsely granular; row of c. 4 large tubercles along the inner disto-ventral angle of merus; laterally projecting oval concave lamella present disto-medially. Inner-dorsal angle of carpus and merus bearing long plumose setae. Ischium and coxa with less dense setae.

Ambulatory legs. Short, P2 $0.8 \times$ length of cheliped. Meri of P2 and P3 completely hidden below lateral extensions of carapace, trigonal in cross-section; carpi and prodopi sub-trigonal; dactyli cylindrical, sparsely granular, with plumose setae and acute chitinous tips. Outer surface of carpi and prodopi similar to outer surface of chelae. Outer surfaces of meri smooth except for P5. Three to five tubercles on the ventro-proximal margins of meri, reducing in size from P2-P5. Legs with marginal plumose setae, longest on dorso-proximal margins of meri.

G1 (Fig. 2A, B). Stout; curved distally, slowly tapering. c. 18 sub-terminal fine, plumose, setae not extending beyond apex; small sub-distal lobe present on inner face; numerous stout, proximally directed, conical setae present on inner and upper faces, several with distinct sockets.

REMARKS

For the purpose of this comparison, *Hepatoporus distinctus* is treated as indistinguishable from *H. guinotae* for reasons given under that species. *H. asper* differs most conspicuously from other species of the genus by the following characters: 1, *H. asper* possesses a concave lateral branchial cavity posterior to the hepatic cavity; 2, the dorsal surface of the carapace in *H. asper* has the regions well separated by deep channels lined with mushroom-shaped tubercles whereas both *H. guinotae* and *H. orientalis* have a much smoother, punctate, or minutely granular surface, with only shallow depressions separating the regions; 3, *H.*

asper bears only two gastric prominences whereas *H. guinotae* bears large tubercles on the supraorbital, gastric, and branchial regions, and the gastric, epibranchial, and cardiac regions of *H. orientalis* are 'protuberant' (Sakai, 1935); 4, the chelipeds and walking legs in *H. asper* bear flattened, often coalesced, fungiform tubercles, giving a coarsely tuberculate appearance whereas on *H. guinotae* and *H. orientalis*, they are merely granular; 5, the third maxillipeds of *H. asper* are covered by small, densely packed, often interconnecting pits whereas those of *H. guinotae* and *H. orientalis* are only granular; 6, the thoracic sternum of *H. asper* has deep erosions that occupy a large portion of each sternite; 7, the abdomen of *H. asper* bears low, fungiform tubercles, that of *H. guinotae* is only granular. Sakai (1935) gives no indication of the nature of the sternum and abdomen in *H. orientalis*; 8, the G1 of *H. asper* (Fig. 2A, B) is distinctly different from that illustrated by Serène (1984: fig. 40) for *H. guinotae*. The new species bears c. 18 subterminal setae that barely reach past the tip. In contrast, the pleopod of *H. guinotae* bears seven setae that extend well beyond the tip. Also the inner face of the G1 of *H. asper* bears a broad, subterminal lobe, which is absent in *H. guinotae*. The G1 is not known for *H. orientalis*.

ETYMOLOGY

From the Latin *asper* = rough or uneven, referring to the deeply pitted and channelled dorsal surface of the carapace.

DISTRIBUTION & HABITAT

Only known from northwestern Australia. Dredged from 40m.

ACKNOWLEDGEMENTS

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MID-DEVONIAN CHONDRICHTHYAN SCALES FROM THE BROKEN RIVER, NORTH QUEENSLAND, AUSTRALIA

ALISON M. DE POMEROY

DePomeroy, A.M. 1994 1201: Mid-Devonian chondrichthyan scales from the Broken River, north Queensland, Australia. *Memoirs of the Queensland Museum* 37(1):87-114. Brisbane. ISSN 0079-8835.

Chondrichthyan scales from mid Emsian to earliest Frasnian of the Dosey-Craigie Platform, Broken River region, northern Queensland include three new form genera, *Gondwanalepis*, *Notiolepis*, and *Aussilepis*, each represented by new species: *G. grossi*, *N. dlenemos*, and *A. lukaso*. Also present are *Cladolepis* sp. cf. *C. gunnelli*, and scales tentatively referred to *Ohiolepis* sp. The diverse fauna includes acanthodian, crossopterygian, palaeoniscoid and thelodont scales; placoderm platelets; onychodontid, palaeoniscoid and indeterminate chondrichthyan teeth; a dipnoan toothplate; and bone fragments of various affinities. □ *Chondrichthyan, Devonian, Eifelian, Givetian, Queensland.*

Alison M. De Pomeroy, Centre for Ecostratigraphy and Palaeobiology, School of Earth Sciences, Macquarie University, New South Wales 2109, Australia; 19 April 1994.

The Broken River Group of north Queensland, covering approximately 320km², is dated late Early to earliest Late Devonian; the biochronology of the area is described by Mawson & Talent (1989). The Dosey-Craigie Platform, from where the new material was collected, is the southernmost of two shallow marine mixed carbonate and siliciclastic shelf sequences in the area (Fig. 1).

Numerous sections of the Dosey-Craigie Platform have been sampled over recent years, leached with acetic acid, and examined for conodonts by the Mawson-Talent team of the Macquarie University Centre for Ecostratigraphy and Palaeobiology (MUCEP); abundant microvertebrate remains have been recovered from these residues. A diverse fauna has been recognised: acanthodian, chondrichthyan, crossopterygian, palaeoniscoid and thelodont scales; placoderm platelets; onychodontid, palaeoniscoid and indeterminate chondrichthyan teeth; a dipnoan toothplate; and bone fragments of various affinities. A description of the chondrichthyan scales is given here; descriptions of other taxonomic groups are in progress. Conodont determinations (Mawson & Talent, 1989) for the mid-Emsian to late-Givetian interval give precise ages for horizons containing the scales.

Fish remains from the Dosey-Craigie Platform occur in several stratigraphic units: the Papilio Formation (shales with subordinate siltstones and nodular limestones - Givetian), the Spanner Limestone Member of the Papilio Formation (bioclastic, well-bedded and frequently nodular limestone - *varcus* Conodont Zone), the Stanley Limestone Member of the Mytton Formation

(bioclastic limestone - late Givetian to earliest Frasnian, late *hermanni-cristatus* to early *asymmetricus* conodont zones), the Lomandra Limestone (mostly calcarenites and calcisiltites - Emsian-Eifelian, *serotinus* to *costatus* conodont zones), the Bracteata Formation (mudstones and lithofeldspathic sandstones, late Emsian *serotinus-patulus* conodont zones), and the Dosey Limestone (calcarenites and calcisiltites, late Eifelian-early Givetian, *kockelianus-ensenensis* conodont zones), Mawson & Talent (1989, fig. 2) summarised the stratigraphic relationships between these units. The Papilio Formation and associated Spanner Limestone Member contain by far the most abundant fish microfossils. These sediments were laid down in deeper water than, for example, the Lomandra and Dosey Limestones, formed under shallow water conditions or possibly sometimes exposed (Mawson & Talent, 1989).

The chondrichthyan scales described herein occur in thirteen sections from the Dosey-Craigie Platform succession - SD15, SD128, SD130, SD131, SD146, SD164, SD170, SD190, SD192, SD196, SD204, SD210, and SD216 (Fig. 2). Table 1 lists the geographical location of the sections. All the scales occur in horizons dated *kockelianus* to *hermanni-cristatus* conodont zones, with two forms extending into the Frasnian *asymmetricus* Conodont Zone (Fig. 3). In addition to possible changes in the fauna through time, this distribution was probably influenced by facies differences (see above). Most taxa have a range spanning all or part of *varcus* Conodont Zone, the age of horizons in the richly fossiliferous Papilio Formation.

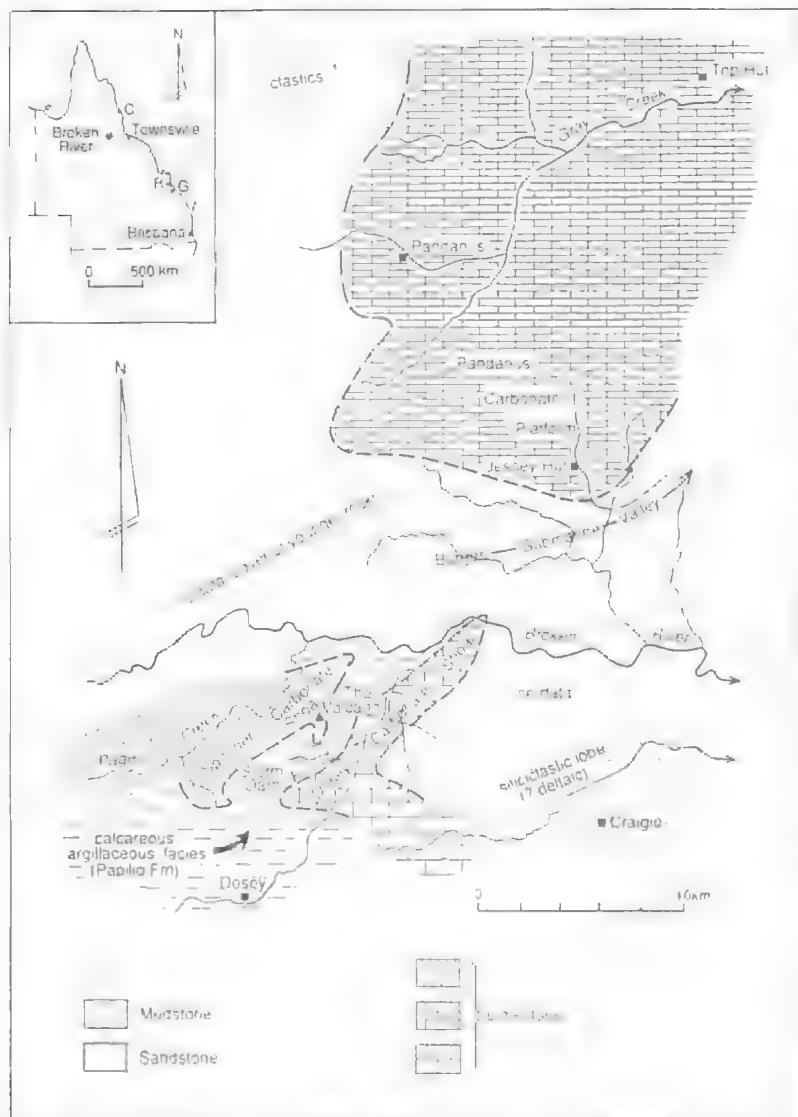


FIG. 1. Palaeogeographic and lithofacies relationships of the Broken River Group during Givetian times (from Mawson and Talent, 1989: fig. 3).

No chondrichthyan scales have been formally described from the Early or Middle Devonian of the Broken River Group, although scales and teeth have been found in acid-leached residues (Turner, 1991; 1993). Turner (1982) described and illustrated shark teeth from the Late Devonian and Early Carboniferous from the northern (Pandanus) platform: *Thrinacodus ferox* Turner, 1982, *Phoebodus* cf. *P. politus* Newberry, 1889, and three species of *Protacrodus*, all dated as "probably Famennian" - and *Stethacanthus thomasi* Turner,

1982 and *Xenacanthus* sp. from the Early Carboniferous. Two new antiarchs, *Wurungulepis denisoni* and *Nawagiaspis wadeae*, were described by Young (1990) from the Broken River Group of the southern (Dosey-Craigie) platform. Turner (1993) reported several forms from the immediate area: an early phoebodont tooth from the Papilio Formation; *Cheiracanthoides comptus* Wells, 1944 scales, onychodontid teeth, palaeoniscoid remains and new shark scales from Fish Hill; turiniids and scales resembling nikoliviids from the Broken River Group; and endemic turiniids, buchanosteid and possibly rhenanid scales, nostolepid scales and platelets and onychodontid teeth from the *pesavis-sulcatus* conodont zones of the underlying Martins Well Limestone.

Remains of chondrichthyans and other groups have been reported from the surrounding region. Turner (1991: fig. 5 i, j) noted and illustrated shark scales and teeth in Middle and Late Devonian limestones from the Broken River area, and reported (Turner, 1993) endemic thelodonts and *Turinia australiensis*

Gross, 1971 from Lochkovian horizons of the Broken River Embayment.

Early and Middle Devonian chondrichthyans have been reported in the literature from other areas of Australia and overseas; forms described as chondrichthyan are summarised (Tables 2, 3). It should be noted, however, that the chondrichthyan affinities of some of these forms have subsequently been questioned.

Localities and sections bear the prefix "SD" for Storm Dam (Fig. 2). Specimens are housed in the

palaeontological collections of the Queensland Museum (QMF).

SYSTEMATIC DESCRIPTION

Subclass CHONDRICHTHYES
Infraclass ELASMOBRANCHII

REMARKS

The scales described below are interpreted as chondrichthyan by the presence of neck canal openings and a bony diamond-shaped base, characters considered diagnostic for the group (Turner, 1991). It is further assumed for the present that the taxa described below belong within the Elasmobranchii, because of overall similarity of scale morphology to that of articulated remains known to belong to elasmobranchs, such as *Antarctilamna prisca* Young, 1982.

Gondwanalepis gen. nov.

ETYMOLOGY

From Gondwana, and the Greek 'lepis' = scale.

DIAGNOSIS

Crown subrhombic or rounded subtriangular, bears eight short parallel ridges deeply dissecting the anterior edge. Posteriorly, crown overhangs base a short way. Neck indented at posterior. Base diamond-shaped or subrectangular, flared into a narrow rim around edges, and gently convex, flat, or gently concave. Six to twelve elliptical openings in posterior neck area.

REMARKS

Gondwanalepis is presumed to be a chondrichthyan because the scales have a diamond-shaped, flat or gently convex base, several neck canal openings at the posterior, and low, narrow, con-

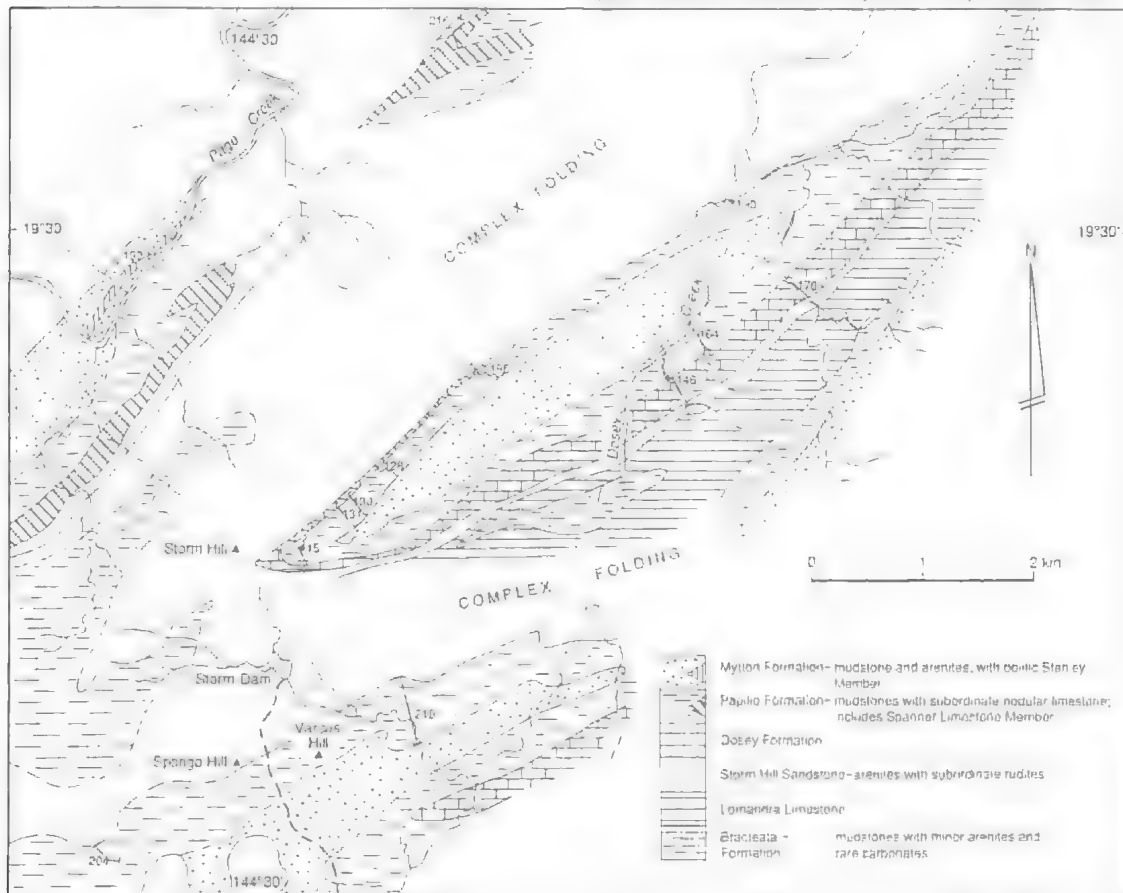


FIG. 2. Broken River Group in the Dosey-Craigie Platform area showing location of stratigraphic sections from which chondrichthyan scales have been recovered (after Mawson & Talent, 1989).

TABLE 1. Geographic localities of the sections mentioned in the text.

| Section | Geographic Locality |
|---------|--|
| SD15 | (North) - Section commences in small gully tributary to Bracteata Creek at WANDO VALE 558388, across small divide to next gully to SW and extending down it to what is approximately axis of Dosey Syncline. (South) - Continuation of preceding section, traversing across other limb of Dosey Syncline, going down section to contact between Storm Hill Sandstone and Dosey Limestone; section ends at WANDO VALE 558384. |
| SD128 | Section through Papilio Formation, commencing in top of Dosey Limestone in a gully at WANDO VALE 566396, crossing it and terminating over next gully to SE at WANDO VALE 568395, approximately 2 km NNE of Storm Dam. |
| SD130 | Section through Dosey Limestone and Papilio Formation; commencing at WANDO VALE 561392, approximately 1.6 km NNE of Storm Dam. |
| SD131 | Section through Dosey Limestone and Papilio Formation, commencing at WANDO VALE 560391, approximately 1.5 km NNE of Storm Dam. |
| SD146 | Section through Dosey Limestone and Papilio Formation, commencing in Camp Gully at WANDO VALE 596400, approximately 4.3 km NE of Storm Dam and aligned down Camp Gully, crossing Dosey Creek to terminate at high escarpment of Mylton Formation. |
| SD164 | Section through to 7m of Dosey Limestone and through Papilio Formation, commencing in GB Gully at WANDO VALE 601401, approximately 4.8 km NE of Storm Dam and aligned down GB Gully, crossing Dosey Creek to terminate at high escarpment of Mylton Formation. |
| SD170 | Section measured in Lomandra Creek, through Bracteata Formation, Lomandra Limestone, Storm Hill Sandstone, Dosey Limestone and basal beds of Papilio Formation, commencing at WANDO VALE 609398, approximately 6.5 km NE of Storm Dam. |
| SD190 | Spot locality in base of Papilio Formation, at WANDO VALE 600420, approximately 300 metres SSW of junction of Dosey and Lomandra Creeks, and approximately 5.7 km NE of Storm Dam. |
| SD192 | Section through Stanley Limestone Member of Mylton Formation, west of Pages Creek to top of ridge, commencing at WANDO VALE 543415, approximately 4 km NNW of Storm Dam. |
| SD196 | Section through Lomandra Limestone, Storm Hill Sandstone and Papilio Formation, commencing at WANDO VALE 574405, approximately 3.2 km NE of Storm Dam. |
| SD204 | Section through Papilio Formation, commencing at head of gully at WANDO VALE 533360, approximately 2.2 km SW of Storm Dam. |
| SD210 | Section through Papilio Formation, commencing at head of gully, tributary to Storm Dam Creek at WANDO VALE 556376, approximately 1 km ESE of Storm Dam. |
| SD216 | Section through Spanner Member of Papilio Formation, commencing at WANDO VALE 546422, approximately 6 km NNE of Storm Dam. |

centric ridges around the posterior margin of the crown. Scale morphology is known in at least 18 genera of Early and Middle Devonian chondrichthyans (Tables 2, 3), but the scales described below cannot be readily referred to any of these.

Wells (1944) assigned scales to three new genera - *Cladolepis*, *Ohirolepis*, and *Deirolepis* - and also illustrated scales of genera *Ctenacanthus*, *Cladoseiache*, and *Cladodus* (Wells, 1944: figs 6, 7, pl. 3, figs 2-21). Scales of *Gondwanalepis* are like none of these. *Cladolepis* scales have a flat, thin crown ornamented by long curved ridges with shorter, overlapping ridges anteriorly; the crown of *Ohirolepis* scales is covered with numerous anteriorly grooved spines (see further discussion below); *Deirolepis* scales have a long neck and thin base; and scales of *Ctenacanthus*, *Cladoseiache*, and *Cladodus* all lack the anterior parallel ridges present on the crown of *Gondwanalepis*.

Gondwanalepis scales are unlike those of *Hercynolepis* in their crown ornamentation. The crown of *Hercynolepis* scales is covered with

short, backwardly-pointing, slightly overlapping ribs (Gross, 1973: pl. 33, figs 13-15), whereas the crown of *Gondwanalepis* has short, parallel, rounded ribs at the anterior. Scales of *Protacrodus*, also discussed by Gross (1973), differ from *Gondwanalepis* in having a low, flat crown, highly convex base, and distinct furrow where the base joins the neck area (Gross, 1973: pl. 32, figs 3-20, pl. 33, figs 1-12).

Scales of *Polymerolepis* were initially considered heterostracan by Karatajute-Talimaa (Obruchev & Karatajute-Talimaa, 1967), but are likely to belong to an Early Devonian shark (Turner & Murphy, 1988). Scales illustrated by Obruchev & Karatajute-Talimaa (1967) and Turner & Murphy (1988) have the crown heavily ornamented from anterior to posterior with many deep ridges, in most specimens parallel, but sometimes radial; this is quite different from the crown ornamentation of *Gondwanalepis*.

From the Emsian *Receptaculites* Limestone, Giffin (1980) figured two scales referred to Karatajute-Talimaa's thelodont *Skannolepis*.

These are now considered to be scales of a new chondrichthyan (Turner, 1993). The scales bear no resemblance to *Gondwanalepis* scales in either shape or ornamentation.

Ellesmereia, erected by Vieth (1980), has ridges extending from the anterior right to the posterior margin of the crown, in contrast to the short anterior ridges of *Gondwanalepis*, and the neck of *Ellesmereia* is more constricted.

Gondwanalepis differs from scales of *Anartecilamna* Young, 1982 in having ridges only at the anterior of the crown, in being generally thicker in lateral view, and in lacking a constricted neck and concave, cup-shaped base.

Pruemolepis, when erected by Vieth-Schreiner (1983), was placed in the acanthodian order Climatida. Mader (1986) transferred the genus to the chondrichthyan subclass Elasmobranchii on the basis of histology. However, *Pruemolepis* scales are now thought to be acanthodian branchial scales (Valiukevicius, pers. comm., 1993). *Pruemolepis* scales have a thicker crown, a more constricted neck, and less conspicuous crown ornamentation than do the scales of *Gondwanalepis*.

Gondwanalepis is unlike the genera from China described by Wang (1984): *Gualepis*, *Chungolepis*, and *Peilepis*. *Gualepis*, unlike *Gondwanalepis*, is characterised by a constricted neck and a dentate posterior margin. *Gualepis*-like scales have been recovered from the late Early Devonian Cravens Peak Beds of the Georgina Basin (Turner, 1993: fig. 8.4g,h). *Chungolepis*, although having a similar lateral view to *Gondwanalepis*, differs by having a strongly convex central rib on the crown forming a long posterior cusp. The crown of *Peilepis* has anterior flutings and is posteriorly bifurcated, and the flat base has a large elliptical pulp opening.

Scales of the genera erected by Mader (1986), *Arauzia*, *Iberolepis* and *Lunalepis*, differ from those of *Gondwanalepis* in their crown ornamentation. The crown of *Arauzia* scales bears one or several thick, stellate, posteriorly-inclined, pointed tubercles. Both *Iberolepis* and *Lunalepis* scales have parallel ridges extending to the posterior margin of the crown. However, the lateral view of one *Lunalepis* scale illustrated by Mader (1986: pl. 4, fig. 9b) is similar to the lateral view of some scales of *Gondwanalepis*.

Gondwanalepis grossi sp. nov. (Figs 4; 5; 6A-C)

ETYMOLOGY

For Walter Gross (1903-1974).

MATERIAL

HOLOTYPE: Scale QMF26084 (Fig. 4A-C).

OTHER MATERIAL: Figured scales QMF26085 - 26093 and 124 other scales.

LOCALITY AND HORIZON

Scales occur at eleven localities in the area (SD15, SD128, SD130, SD131, SD146, SD164, SD170, SD196, SD204, SD210, SD216 - Fig. 2), in horizons of the Papilio Formation and its associated Spanner Limestone Member, and the Dosey Limestone, ranging in age from *cockelianus* to *hermanni-cristatus* conodont zones.

DIAGNOSIS

As for genus (this is the only species).

REMARKS

The lateral view of *Gondwanalepis* scales is similar to that of both *Changolepis tricuspidus* Wang, 1984 from the Early Devonian of south-west

| DEVONIAN | | | | | | | Chondrichthyan | | | | | |
|-----------|----------|-----------|----------------|-----------|--------|----------|----------------|---------|------------|--|--|------|
| MIDDLE | | | | | C | SERIES | | | | | | |
| Eifellian | | Givetian | | | | | | | Fr. | STAGE | | |
| | | | | | | | | | | | | ZONE |
| parvus | costatus | australis | hormensis s.s. | hormensis | varcos | hermanni | disparis | lobatus | asymmetrus | | | |
| | | | | | | | | | | <i>Gondwanalepis grossi</i> | | |
| | | | | | | | | | | <i>Natolepis dienemos</i> var. 1 | | |
| | | | | | | | | | | var.2 | | |
| | | | | | | | | | | var.3 | | |
| | | | | | | | | | | <i>Aussilepis lukaso</i> | | |
| | | | | | | | | | | <i>Ohiolepis</i> sp. | | |
| | | | | | | | | | | <i>Cladolepis</i> sp. cf. <i>C. gunnelli</i> | | |
| | | | | | | | | | | Chondrichthyan A | | |
| | | | | | | | | | | Chondrichthyan B | | |

FIG. 3. Relative ranges of chondrichthyan taxa.

China (Wang, 1984: fig. 12f) and *Maplemillia costata* Gross, 1973 from the Late Devonian of Iowa (Gross, 1973: pl. 30 fig. 1d). In all three cases, the gently convex base is flared into a rim around the edge, the neck is deeper at the back, and the crown slopes up and back from the anterior of the base, with no anterior edge on the crown. But *Gondwanalepis* differs from *Changolepis* and *Maplemillia* in the crown ornamentation; neither of these genera has short, parallel ridges on the crown.

The short, deep, parallel ridges on the crown of *Gondwanalepis* are similar to the ornamentation on some acanthodian scales, e.g. *Cheiracanthoides comptus* Wells, 1944 illustrated by Giffin (1980: fig. 5), or *Cheiracanthoides* sp. cf. *comptus* illustrated by Boucot et al. (1989: fig. 19). However, in *Cheiracanthoides* scales the crown is more pointed posteriorly, and the base more convex. The original generic diagnosis for *Cheiracanthoides* of Wells (1944) includes several characters which could be confused with those of *Gondwanalepis*. *Cheiracanthoides* scales have radiating ridges usually extending at least halfway to the posterior corner of the crown, which has a well-defined anterior edge (Wells, 1944: fig. 3). However, the grooves between the ridges are not deep enough to notch the anterior margin deeply, the scales have a well-developed neck, and there are no neck canals. In contrast, scales of *Gondwanalepis* have parallel ridges which are shorter than in *Cheiracanthoides*, the crown has no anterior edge, and the ridges continue down over the front of the scale, where they notch the margin deeply. The neck is not well-developed, being indented only at the posterior. In addition, *Gondwanalepis* scales always lack the concentric ridges on the base, which are typical of acanthodian scales (Gross, 1973).

MEASUREMENTS

The scales vary in length between 0.3mm and 0.8 mm, and in height between 0.3mm and 0.7

mm. The width of most scales is between 0.6mm and 0.8mm, but the range extends from 0.45mm to 1.1mm. The length/width ratio ranges from 0.5 in the particularly wide, high scales with the subrectangular, concave base, to 1.0 in the relatively longer scales with the diamond-shaped, convex base. Approximately 75% of the scales in the available sample have width greater than length. The remaining scales have equal width and length.

DESCRIPTION

Morphology. The crown bears eight short sub-parallel ridges. The ridges deeply dissect the anterior edge of the crown, extending down almost to the flared rim around the base. In some particularly wide specimens, with a gently curved anterior margin, the ridges are extremely deep, and give the edge of the scale a scalloped appearance (Fig. 4M-O). The anterior edge of the scale is variably curved, ranging from approximately 90° to 150°. Only 4% of the scales in the available sample have the anterior edge gently curved (Fig. 4M-O); 60% of the scales have the anterior edge moderately curved (Fig. 4A-C, G-I); the remaining scales (36%) have a more sharply curved anterior margin (Fig. 5A-C).

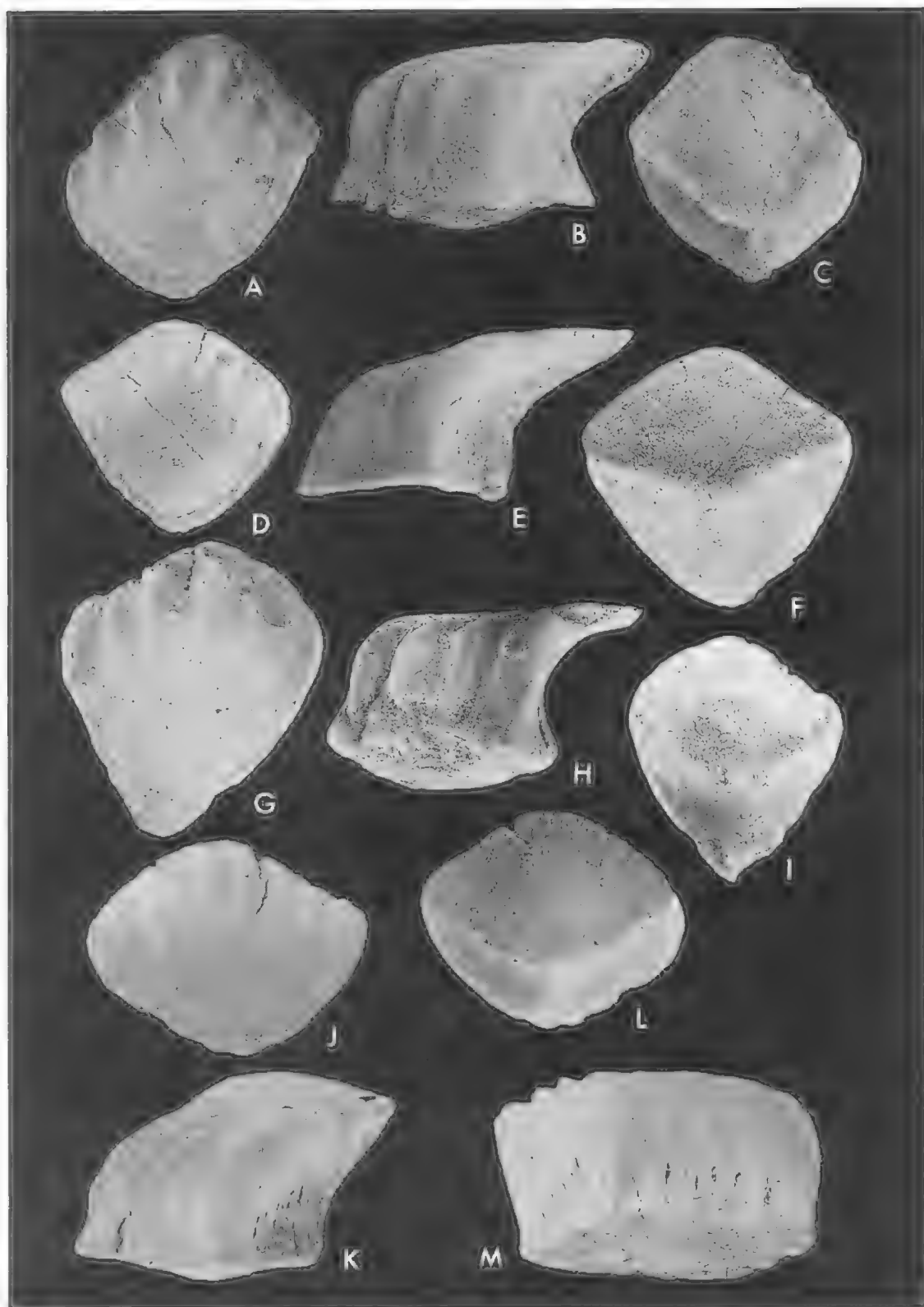
The central ridges extend back from the anterior margin for about one-third the length of the crown. The outer ridges continue as low, narrow curved ridges parallel to the lateral and posterior margins of the crown (Fig. 4A). There may be up to four of these concentric ridges in the posterior section. The anterior margin of the crown is high; the crown slopes slightly upwards posteriorly and extends only a short way beyond the posterior of the base (Fig. 4B,E).

The neck is not clearly defined, although all scales are high, particularly those that are wider than they are long. The neck area is indented posteriorly, and shows up to 12 elliptical canal openings (Fig. 5M,6C). A single row of small circular openings around the lower part of the

FIG. 4. *Gondwanalepis grossi* gen. et sp. nov. A-C, holotype, scale QMF26084 from SD164/19; D-F, scale QMF26085 from SD216/106.1; G-I, scale QMF26086 from SD164/18; J-L, scale QMF26087 from SD128/212 (50 paces north); M-O, scale QMF26088 from SD128/210. A, crown view, x60; B, lateral view, x95; C, basal view, x60; D, crown view, x50; E, lateral view, x75; F, basal view, x45; G, crown view, x45; H, lateral view, x70; I, basal view, x45; J, crown view, x60; K, lateral view, x90; L, basal view, x60; M, crown view, x75; N, lateral view, x90; O, latero-basal view, x90.

FIG. 5. *Gondwanalepis grossi* gen. et sp. nov. A-C, scale QMF26089 from SD204/174; D-F, scale QMF26090 from SD164/18; G-I, scale QMF26091 from SD210/9; J-M, scale QMF26092 from SD204/168. A, crown view, x55; B, lateral view, x65; C, basal view, x50; D, crown view, x50; E, lateral view, x90; F, basal view, x60; G, crown view, x60; H, lateral view, x75; I, basal view, x50; J, crown view, x40; K, lateral view, x60; L, basal view, x40; M, posterior view, x50.





anterior neck area is visible in some specimens (Fig. 6A).

The base is most commonly diamond-shaped (Fig. 4C, F, I, L), but may be subrectangular (Fig. 4N-O). These represent the ends of a continuous range of morphological types. The diamond-shaped bases are usually gently convex, or sometimes flat, and flared into a narrow rim around the edges. The subrectangular bases are gently concave. All the scales are high relative to the crown area, but this is particularly noticeable in those specimens with the concave, subrectangular base (Fig. 4N-O).

Histology. The base of cellular bone extends in an inverted cone shape high into the scale (Figs 11A,B). This tissue contains osteocytes aligned both concentrically and radially (Fig. 11B). The crown appears to consist of discrete increments added anteriorly and posteriorly to a central initial element (arrow in Fig. 11C). This type of apposed growth is typical of complex chondrichthyan scales (Zangerl, 1981), in contrast to the concentric growth pattern in most acanthodian scales (Dension, 1979); one exception is the acanthodian *Nostolepis robusta* (Brotzen), 1934 described by Gross (1971a) – these scales show some apposition of crown elements. The posterior section of the crown consists of cellular material (Fig. 11D) similar in appearance to the Stranggewebe in acanthodian climatiid scales such as *Cheiracanthoides comptus* Wells, 1944 (e.g. Gross, 1973: fig. 5b,c). This nostolepid-type histology typical of climatiids is also seen in some early cladolepid chondrichthyans (J. Vergoossen, pers. comm., 1994).

DISCUSSION

It is possible that differently shaped scales are of different ages, or occur on different parts of the body. The wide, short scales (Fig. 4M) have a similar width range to the longer scales (Figs 4A,D, 5G). Complex shark scales grow by adding new growth elements around the margins

(Zangerl, 1981); it is conceivable that the scale depicted in Fig. 4M is a young scale that could have grown further by additions at the anterior and posterior (see discussion of histology above), resulting in a scale with a more curved anterior margin, longer anterior ridges on the crown, and a longer posterior section to the crown (Figs 4A-C, 4G-I, 5G-I).

Notiolepis gen. nov.

ETYMOLOGY

From the Greek 'notios' = southern, and 'lepis' = scale.

DIAGNOSIS

Crown oval or subrectangular, bearing four to eight parallel anterior ridges. Crown joins directly onto base anteriorly, and slopes up towards posterior. Neck not indented, and has six to twelve canal openings along posterior. Base rhombic or suboval, flat or concave, with no rim around the edge.

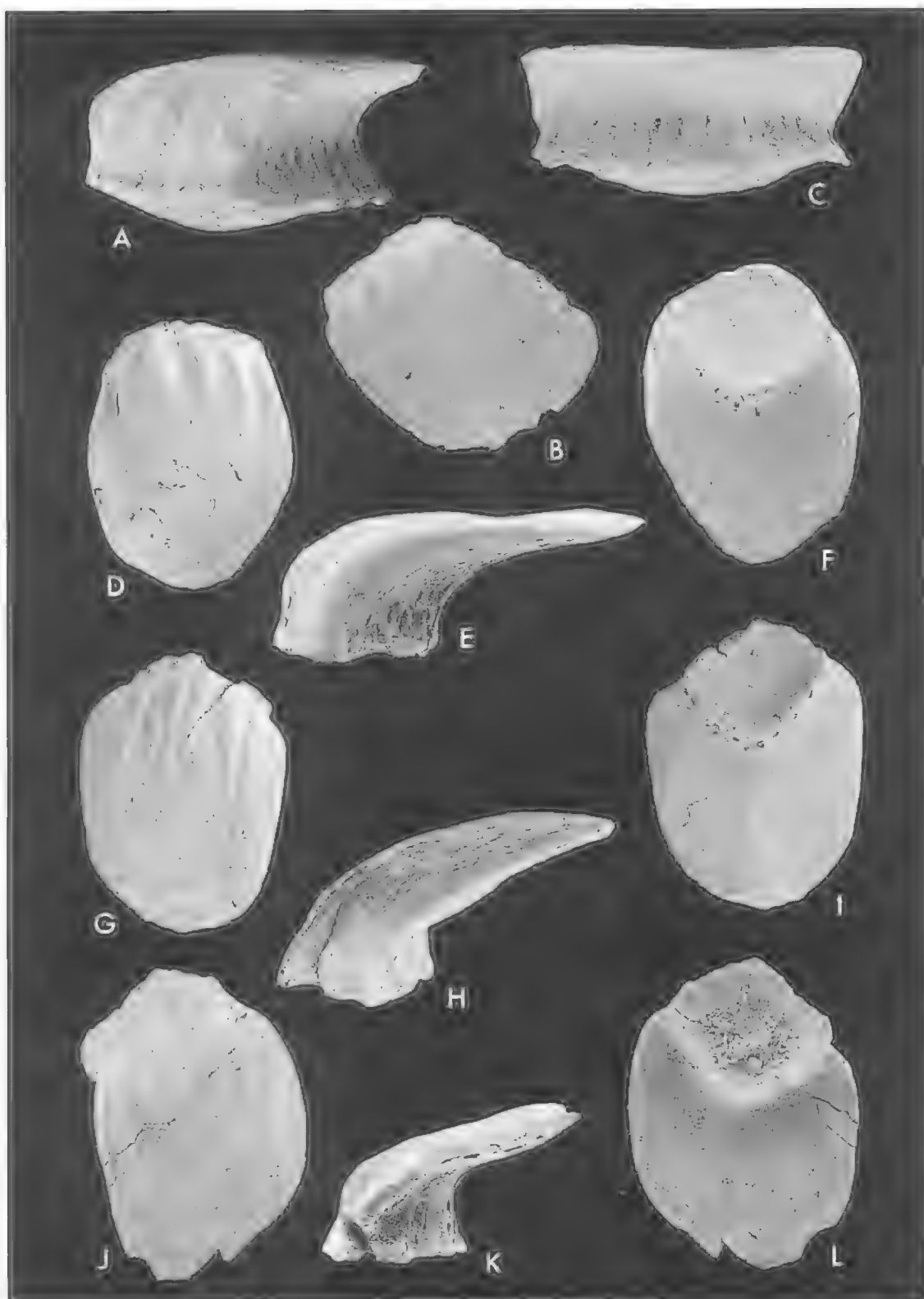
REMARKS

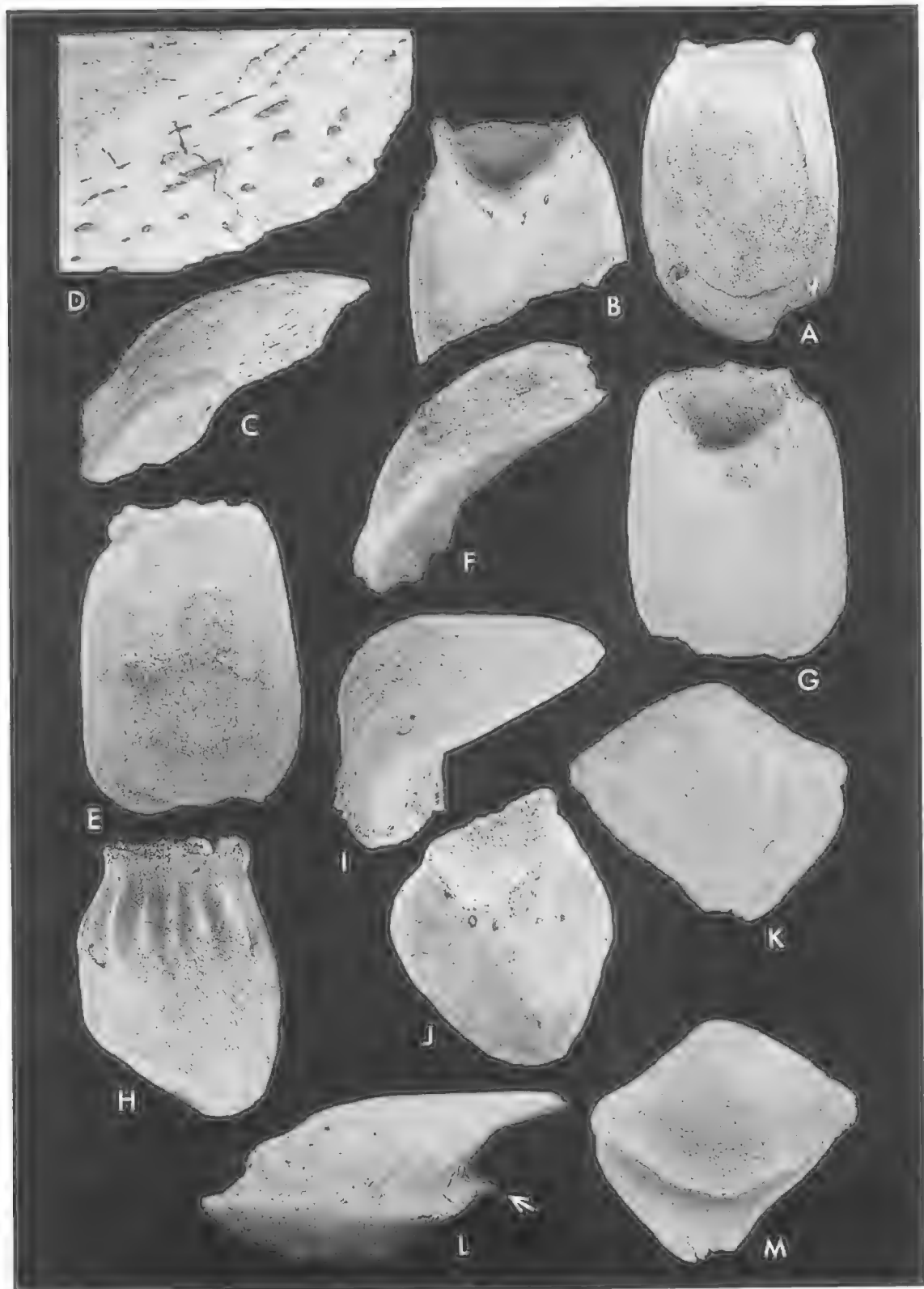
The scales of *Notiolepis* are distinguished from those of *Gondwanalepis*, described above, by the following characters: the crown is relatively longer compared with the width; the anterior ridges on the crown are less pronounced; the neck has the same thickness as the base, rather than being indented as in *Gondwanalepis*; and the base lacks a rim around its edge. These seem to be consistent differences, even though there is variation in crown shape within each genus, which may indicate scales from different parts of the body. On the available small sample, *Notiolepis* is therefore considered to be a separate taxon, although this assessment may change as more material becomes available.

Notiolepis gen. nov. as defined here may be distinguished from previously described genera in the type of crown ornamentation; the six genera

FIG. 6. A-C, *Gondwanalepis grossi* gen. et sp. nov., scale QMF26093 from SD204/174. D-L, *Notiolepis dienemos* gen. et sp. nov. Var. 1. D-F, holotype, scale QMF26094 from SD15/81; G-I, scale QMF26095 from SD204/119.5. J-L, scale QMF26096 from SD204/174. A, lateral view, x 75; B, crown view, x 50; C, posterior view, x 65; D, crown view, x 45; E, lateral view, x 65; F, basal view, x 50; G, crown view, x 50; H, lateral view, x 65; I, basal view, x 50; J, crown view, x 90; K, lateral view, x 90; L, basal view, x 90.

FIG. 7. A-J, *Notiolepis dienemos* gen. et sp. nov. Var. 2. K-M, *Cladolepis* sp. cf. *C. gunnelli*. A-D, scale QMF26097 from SD128/212+ (150 paces N) – specimen broken during SEM photography; E-G, scale QMF26098 from SD128/217; H-J, scale QMF26099 from SD128/202.3. K-M, scale QMF26100 from SD190/60. A, crown view, x 55; B, basal view, x 60; C, posterolateral view, x 75; D, detail of broken edge, x 275; E, crown view, x 70; F, lateral view, x 75; G, basal view, x 70; H, crown view, x 55; I, lateral view, x 60; J, basal view, x 55; K, crown





described and illustrated by Wells (1944): *Cladolepis*, *Ohiolepis*, *Deirolepis*, *Ctenacanthus*, *Cladoselache*, and *Cladodus*; *Hercynolepis* and *Protacrodus* described and illustrated by Gross (1973); *Polymerolepis* figured by Obruchev & Karatajūte-Talimaa (1967) and Turner & Murphy (1988); '*Skamolepis*' (Giffin, 1980; Turner, 1993); *Ellesmerella* and *Pruemolepis* (Vieth, 1980; Vieth-Schreiner, 1983); *Antarctilamna* (Young, 1982); the three genera from China, *Gualepis*, *Changolepis*, and *Peilepis* (Wang, 1984); and the Spanish *Iberolepis* and *Lunalepis* (Mader, 1986). No scales of these genera have the short, parallel ribs on the anterior section of the crown, with the posterior part of the crown smooth, as in *Notiolepis*. *Notiolepis* also differs from most of these other chondrichthyan genera in lateral and basal views. *Notiolepis* scales have a similar lateral view to scales of *Ctenacanthus costellatus* Traquair, 1884, *Peilepis solida* Wang, 1984, and *Iberolepis aragonensis* Mader, 1986; the differences between *Notiolepis* and these genera are discussed below.

***Notiolepis dienemos* sp. nov.**
(Figs 6D-L; 7A-J; 8A-F)

ETYMOLOGY

From the Greek '*dienemos*' = windswept, referring to the appearance of the crown.

MATERIAL

HOLOTYPE: Scale QMF 26094 (Fig. 6D-F).

OTHER MATERIAL: Variety 1: Figured scales, QMF26095 & 26096, and 24 other scales.

Variety 2: Figured scales, QMF26097-9, and seven other scales.

Variety 3: Figured scales, QMF26101-2, and five other scales.

LOCALITY AND HORIZON

All specimens were recovered from the Papilio Formation, Spanner Limestone or Stanley Limestone. Variety 1 occurred at five localities (SD15, SD128, SD204, SD210, SD216 - Fig. 2) in horizons ranging in age from mid- *envensis* to *hermanni-cristatus* conodont zones; Variety 2 at two localities (SD128, SD210) in *varcus* Conodont Zone; and Variety 3 at five localities (SD15, SD128, SD192, SD204, SD210) in *kockelianus*, lower and middle *varcus*, and *asymetricus* conodont zones.

DIAGNOSIS

As for genus (only species).

MEASUREMENTS

Variety 1: scale length varies between 0.5mm and 0.9mm; width ranges from 0.4mm to 0.7mm; height ranges from 0.2mm to 0.3mm. The length/width ratio is 1.17 to 1.29.

Variety 2: length of the crown ranges from 0.7mm to 0.9mm, and width from 0.5mm to 0.6mm. The length/width ratio ranges from 1.4 to 1.6.

Variety 3: the crown length is 0.6mm to 0.7mm, the width is 0.7mm to 0.8mm, and the length/width ratio is 0.86 to 0.87.

DESCRIPTION

Morphology. Three varieties of scales have been grouped together on the basis of their similar lateral views (Figs 6E,H,K; 7F,I; 8B,E).

In Variety 1, (Fig. 6D-L), the crown is oval shaped, with both anterior and posterior edges gently curved. The crown bears four to seven long parallel ridges, usually starting at the anterior edge and extending posteriorly approximately half to two-thirds the length of the crown. In some specimens, the base extends slightly anteriorly, to give a smooth anterior margin to the scale in dorsal view (Fig. 6J). In these specimens, the parallel ridges do not extend right to the anterior margin of the scale, and the crown extends further beyond the base posteriorly than in the specimens lacking the anterior basal extension. The base is diamond-shaped, and either flat or gently concave. Up to 12 neck canal openings are found at the posterior.

In Variety 2 (Fig. 7A-J) the crown is subrectangular, thin, and slopes steeply upward from a fairly straight anterior edge to a gently rounded posterior margin. The crown bears four to seven parallel ridges, extending from just behind the anterior edge, back to approximately mid-way towards the posterior (Fig. 7E,H). The neck area is not indented. The base is a concave, narrow semi-diamond or semi-oval shape, and, like the crown, is straight along the anterior margin (Fig. 7B,G). The general appearance of the scale is wide, flat and high, with only the base area appearing to have much volume. Specimen QMF26097 was broken during SEM photography, revealing numerous pulp canals within the crown (Fig. 7D), typical of the composite type of chondrichthyan scale described by Zangerl (1981), where each new growth element has its own vascular supply.

Variety 2 scales mainly differ from those of Var. 1 in their base. The base of Var. 1 scales is flat or gently concave, and diamond-shaped. The

TABLE 2. Reported chondrichthyans from the Early and Middle Devonian of Australia

| Taxa | Locality | Age | Material | Reference |
|---|--|---|---|-------------------------------------|
| <i>Antarctilamna</i> sp. | Bunga Beds | Late Giv. - early Fras. | teeth, fin spines, scales, dermal denticles, endocrania & jaw | Young, 82; Long, 91; Turner, 91; 93 |
| cf. <i>Gualepis</i> | Cravens Peak | | scales | Turner, 91; 93 |
| ? <i>Memurdodus</i> cf. <i>featherensis</i> | Bunga Beds | Late Giv. - early Fras. | teeth | Young, 82 |
| <i>Memurdodus whitei</i> | Cravens Peak | Eifelian | teeth | Turner & Young, 87; Turner, 93 |
| <i>Ohiolepis</i> sp. | Jerula Fm., Trundle Beds, Dulladerry Rhyolite, Mt. Dam Limestone | Lochkovian | | Turner, 93 |
| | Tumblong | Pragian | denticles | Pickett et al., 85 |
| | Tumblong | Emsian | | Turner, 93 |
| | <i>Receptaculites</i> Limestone | ? Late Emsian | scales | Giffin, 80 |
| | Murrumbidgee & Buchan Lsts. | Late Ems. - early Fras. | scales | Turner, 82 |
| | Mt. Frome Limestone | <i>serotinus/patulus</i> Zones - early Eifelian | | Turner, 93 |
| | Taemas - Buchan | Emsian (<i>dehiscens</i> - <i>serotinus</i>) | | Young, 93 |
| ' <i>Skamolepis</i> ' sp. | <i>Receptaculites</i> Limestone | Late Emsian | scales | Giffin, 80 |
| | Jesse Limestone | Late Emsian (<i>perbonus</i> - <i>laticostatus</i>) | scales | Turner, 93 |
| | Mt. Frome Limestone | <i>serotinus</i> - <i>patulus</i> Zones | scales | Turner, 93 |
| <i>Xenacanthus</i> sp. | Bunga Beds | Late Givetian - Early Frasnian | teeth | Young, 82 |
| Possible occurrences: | | | | |
| cf. <i>Antarctilamna</i> | Silverband Fm., Grampians | Gedinnian - early Frasnian | scales, fin spines, tooth whorls | Turner, 86 |
| Neoselachian-like | Trundle Beds | ? Late Lochkovian | scale | Turner, 91; 93 |
| shark | Bunga Beds | Mid Devonian | articulated or semi-articulated cartilage remains | Long, 91 |
| possible shark | Buchan Gp. & Pt. Hibbs Lst. | Pragian | scales | Turner, 93 |

base of Var. 2 scales is deeply concave, and a narrow half-diamond or semi-oval shape, with the anterior edge of the base fairly straight.

In Variety 3 (Fig. 8A-F) the crown is fairly straight across the anterior, but rounded at the posterior (Fig. 8D). The front of the crown slopes up steeply from the base, then levels out and slopes up more gradually towards the posterior margin (Fig. 8B). Seven short parallel ridges occur on the steeply sloping anterior edge of the crown. The posterior part of the crown is flat, thin and unornamented. The neck is not constricted. The base is a flat, narrow rhombic shape (Fig.

8C,F). Six to eight elliptical neck canal openings occur on the underside of the crown, just behind the base. The overall appearance of these scales is wide, flat, and low. The crown is wider than it is long.

Variety 3 scales differ from Var. 1 and Var. 2 in the shape of both the base and the crown. The base here is flat and narrowly rhombic, in contrast with the diamond-shaped flat or gently concave base of Var. 1, and the narrow half-diamond- or semi-oval-shaped deeply concave base of Var. 2. The crown of Var. 3 scales is straight at the anterior edge, widely rounded at the posterior

edge, and bears seven short parallel ridges only at the very front of the scale. The crown of Var. 1 and Var. 2 bears parallel ridges extending much further back towards the posterior. The angle of inclination of the crown varies between individual scales but is similar in all three varieties of *Notiolepis*. However, each of the three varieties has the length/width ratio falling within a distinctive range, reflecting a general difference in overall scale shape between the three varieties: 1.17-1.29 for Var. 1, 1.4-1.6 for Var. 2, and 0.86-0.87 for Var. 3.

Histology. Scales consist of a conical bony base (Fig. 12A), containing osteocytes and fine radial fibres (Fig. 12B). The cellular crown material is attached to the posterior edge of the basal cone (Fig. 12A). The crown, like that of *Gondwanalepis*, appears to grow by apposition of discrete elements (Fig. 12B), and these crown elements also consist of material similar in appearance to Strangewebe (Fig. 12C).

DISCUSSION

Notiolepis scales are similar in lateral view to the scales of the chondrichthyans *Ctenacanthus costellatus* Traquair, 1884 (Reif, 1978: fig. 1a), *Peilepis solida* Wang, 1984 (Wang, 1984: figs 14, 15), and *Iberolepis aragonensis* Mader, 1986 (Mader, 1986: pl. 4, fig. 2c). *Notiolepis* scales differ from *C. costellatus* Traquair, 1884 scales by lacking the constricted neck and flared base, and having less pronounced, but a greater number of, anterior ridges on the crown. The *P. solida* Wang, 1984 scales have an anteriorly protruding base, a large basal cavity, a posteriorly bifurcated crown, and three flutings on the anterior crown surface, all of which are absent in *Notiolepis*. The base of *I. aragonensis* Mader, 1986 is longer and flatter than that of *Notiolepis*, and the crown ornamentation is different.

Specimens of *Notiolepis* with the concave base (Var. 1) resemble those of *Antarctilamna prisca* Young, 1982 in basal view (Young, 1982: fig. 4e). However, *Notiolepis* Var. 1 scales differ in having a more gently concave base, lacking a constricted neck, and having parallel ridges in the anterior part of the crown rather than concentric

ridges over the whole crown forming short cusps along the posterior margin. Variety 2 scales also have a basal view similar to that of *A. prisca* Young, 1982, except that the concave cup-like base is narrower.

In lateral view, *Notiolepis* scales may perhaps be confused with some thelodont scales, for example *Turinia* sp. (Young et al., 1987: fig. 5b) or *Canonis grossi* Vieth, 1980 (Vieth, 1980: pl. 3, fig. 3c). However, the *Notiolepis* scales lack the thick, rounded base encircling the lower edge of the scale, the large basal cavity and the single pulp canal opening typical of thelodont scales. In addition, the posterior part of the crown is thinner and flatter, and the crown bears ridges only at the anterior edge, not laterally as is the case with the *Turinia* sp. scales figured by Young et al. (1987). Scales of *C. grossi* Vieth, 1980 have a round, gently convex base in ventral view, and three pronounced ridges covering the length of the crown and extending into three denticles at the posterior margin in dorsal view. *Notiolepis* scales, in contrast, have a rhombic, flat or concave base, ridges only in the anterior part of the crown, and a smoothly rounded posterior margin.

Aussilepis gen. nov.

ETYMOLOGY

From the local colloquial word Aussie, and the Greek 'lepis' = scale.

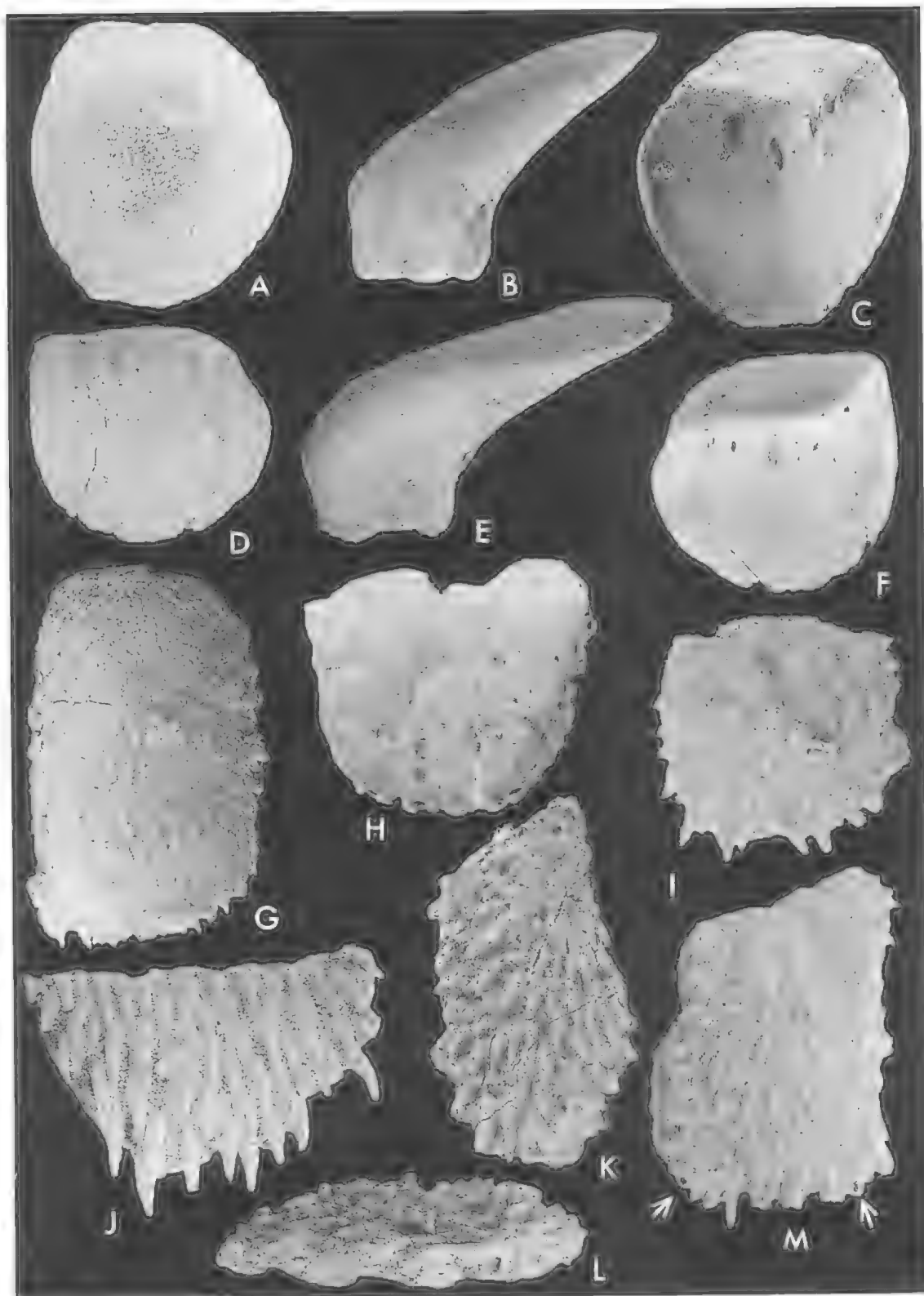
DIAGNOSIS

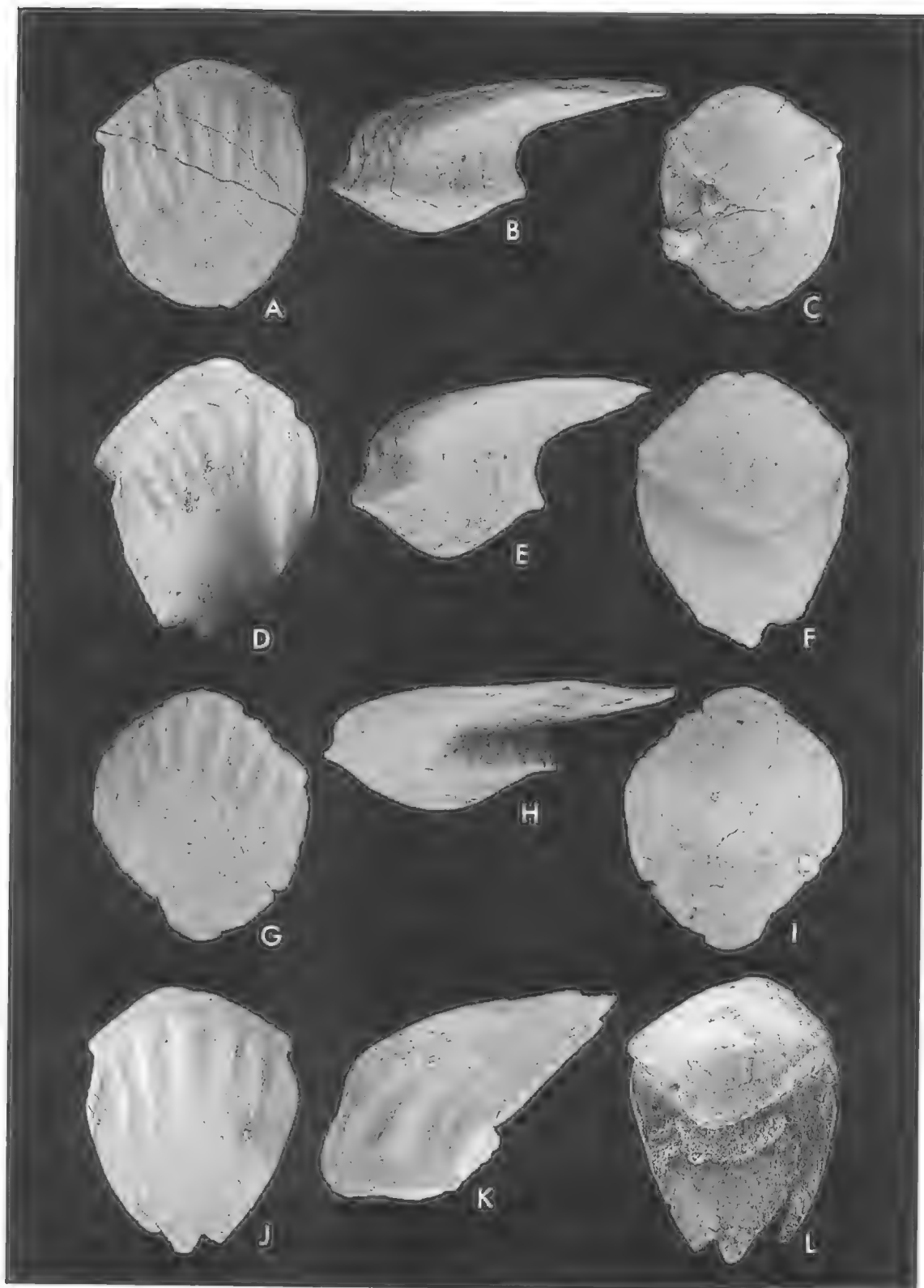
Crown subcircular, extends beyond base posteriorly. Eight thick, deep ridges extend from anterior edge to approximately middle of crown. Neck shallow, slightly indented at anterior and posterior. Approximately six to ten small openings in posterior part of neck. Base diamond-shaped, convex.

REMARKS

The scales of *Aussilepis* resemble those of *Gondwanalepis* in the deep anterior ridges on the crown, and in the narrow rim around the margin of the base, this latter feature distinguishing these two genera from *Notiolepis*. However, *Aussilepis*

FIG. 8. A-F, *Notiolepis dienemos* gen. et sp. nov. Var. 3; G-M, *Ohiolepis* sp. A-C, scale QMF26101 from SD128/212; D-F, scale QMF26102 from SD204/174; G, scale QMF26105 from SD128/144.2; H, scale QMF31828 from SD204/174 upslope; I, scale QMF26104 from SD216/99.8; J, broken scale QMF31829 from SD204/174 upslope; K-L, scale QMF26103 from SD130/262.5; M, scale QMF31830 from SD204/174 upslope. A, crown view, x 60; B, lateral view, x 85; C, basal view, x 60; D, crown view, x 50; E, lateral view, x 95; F, basal view, x 50; G, crown view, x 25; H, basal view, x 45; I, crown view, x 35; J, crown view, x 60; K, crown view, x 45; L, lateral view, x 60; M, crown view, x 45.





differs from *Gondwanalepis* in the following features: the posterior part of the crown is smooth, thin, and lacks the narrow ridges parallel to the posterior margin; the crown overhangs the base further posteriorly; the base is more convex; and the outer ridges of the crown are less thickened (Fig. 9B,E,H) in contrast to *Gondwanalepis* (Figs 4B,K; 5E,K).

Aussilepis scales are distinguished from *Notiolepis* scales by the differences in neck and base; *Aussilepis* has a slightly indented neck and convex base, while in *Notiolepis* the neck and base are the same size, with the base being either flat or concave. The base of *Notiolepis* scales occupies a smaller proportion of the length of the scale than with *Aussilepis* scales.

These scales have been assigned to a new genus because their morphology is unlike that of previously described scales (Tables 2, 3). As with *Gondwanalepis* and *Notiolepis*, it is the crown ornamentation that differs most from previously described genera. The crown of *Aussilepis* has short, deep ridges and furrows at the anterior margin, while the posterior section of the crown is unornamented (except for occasional low markings, similar to growth rings, parallel to the posterior margin Fig. 9J). *Cladolepis* scales (Wells, 1944) have a flat, thin crown ornamented by long curved ridges with shorter, overlapping ridges anteriorly. The crown of *Ohiolepis* scales is covered with numerous anteriorly grooved spines (Wells, 1944). *Deirolepis* scales (Wells, 1944) have a long neck and thin base. Scales of *Ctenacanthus*, *Cladoseleache*, and *Cladodus*, as figured by Wells (1944), all lack the anterior parallel ridges present on the crown of *Aussilepis*. The crown of *Hercynolepis* scales is covered with short, backwardly-pointing, slightly overlapping ribs (Gross, 1973). *Protacrodus* scales have a low, flat crown, deeply convex base, and distinct furrow where the base joins the neck area (Gross, 1973). Scales of *Polymerolepis* have the crown ornamented with many deep parallel or radiating ridges (Obruchev & Karatajute-Talimaa, 1967; Turner & Murphy, 1988). Scales described as '*Skamolepis*' by Giffin (1980) differ from those of *Aussilepis* in general shape and ornamentation. Scales of *Ellesmereia* (Vieth, 1980) have ridges extending from the anterior right to the posterior margin of the crown, and the neck of *Ellesmereia*

is more constricted. *Aussilepis* lacks the constricted neck, the concave, cup-shaped base, and distinctive curved ridges on the crown of *Antarctilamna* (Young, 1982), and is thicker in lateral view. *Pruemolepis* scales (Vieth-Schreiner, 1983; Mader, 1986) have a thicker crown, a more constricted neck, and less conspicuous crown ornamentation than those of *Aussilepis*. *Gualepis* (Wang, 1984) is characterised by a constricted neck and a dentate posterior margin. *Changolepis* (Wang, 1984) has a strongly convex central rib on the crown forming a long posterior cusp. The crown of *Peilepis* (Wang, 1984) has anterior flutings and is posteriorly bifurcated, and the flat base has a large elliptical pulp opening. Scales of both *Iberolepis* and *Lunalepis* (Mader, 1986) have parallel ridges extending to the posterior margin of the crown.

Aussilepis lukaso sp. nov.

(Fig. 9)

ETYMOLOGY

From the languages of the Koori (original inhabitants of Australia) 'luk' = like, and 'kaso' = another, referring to the similarity between the lateral view of these scales and that of some other taxa.

MATERIAL

HOLOTYPE: Scale QMF26106 (Fig. 9A-C).

OTHER MATERIAL: Figured scales, QMF26107-9 and 75 other scales.

LOCALITY AND HORIZON

Scales occur at eight localities (SD15, SD128, SD146, SD164, SD196, SD204, SD210, SD216 - Fig. 2), in horizons of the Papilio Formation and its associated Spanner Limestone Member dated from *ensensis* to *hermanni-cristatus* conodont zones.

DIAGNOSIS

As for genus (this is the only species).

MEASUREMENTS

Scales range in length from 0.5mm to 0.9mm; in width from 0.4mm to 0.9mm; and in height from 0.3mm to 0.45mm. The length/width ratio ranges from 1.0 to 1.33.

FIG. 9. *Aussilepis lukaso* gen. et sp. nov. A-C, holotype, scale QMF26106 from SD204/174; D-F, scale QMF26107 from SD204/174; G-I, scale QMF26108 from SD204/174; J-L, scale QMF26109 from SD210/30; A, crown view, x 50; B, lateral view, x 70; C, basal view, x 45; D, crown view, x 50; E, lateral view, x 60; F, basal view, x 50; G, crown view, x 45; H, lateral view, x 60; I, basal view, x 45; J, crown view, x 60; K, lateral view, x 75; L, basal view, x 60.

TABLE 3. Reported chondrichthyans from the Early and Middle Devonian from overseas.

| Taxa | Locality | Age | Material | Reference |
|--|---|--------------------------------|---------------------------|-----------------------|
| <i>Antarctilamna prisca</i> | Aztec Siltstone, Antarctica | Givetian | fin spines, scales, teeth | Young, 82; 89; 91 |
| <i>A. seriponensis</i> | Catavi Fm., Bolivia | Late Early - Mid. Devonian | fin spine | Gagnier et al., 88 |
| | Santa Rosa Fm., Bolivia | Lochkovian - Pragian | fin spine | Lelievre et al., 93 |
| <i>Antarctilamna</i> sp. | Wajid Sandstone, Iran | Pragian | scales | Forey et al., 92 |
| | Sicasia & Belen Fms., Bolivia | Mid. Devonian | fin spine | Lelievre et al., 93 |
| | Khush - Yeilagh Pass, Bolivia | Emsian - Eifelian | fin spine | Lelievre et al., 93 |
| <i>Arauzia federicoi</i> | Spain | Early Devonian | scales | Mader, 86 |
| <i>Bolivacanthus sagittalis</i> | Catavi Fm., Bolivia | Late Early - Mid. Devonian | spine fragment | Gagnier et al., 88 |
| | Santa Rosa Fm., Bolivia | Lochkovian - Pragian | fin spine | Lelievre et al., 93 |
| <i>Changolepis tricuspidus</i> | Xitun Member, Sth China | Early Devonian | scales | Wang Nianzhong, 84 |
| <i>Cladodus (Protacrodus) wildungensis</i> | Cincinnati Arch region, US | Mid. Devonian | scale | Wells, 44 |
| <i>Cladolepis gunnelli</i> | Cincinnati Arch region, US | Mid. Devonian | scales | Wells, 44 |
| | Indiana, US | Early Mid. Devonian | scales | Gross, 73 |
| <i>?C. gunnelli</i> | Lauch Fm., Germany | Early Eifelian | scale | Vieth - Schreiner, 83 |
| <i>C. ornata</i> | Cincinnati Arch region, US | Mid. Devonian | scale | Wells, 44 |
| <i>Cladolepis</i> sp. | Spain | Early Devonian | scales | Mader, 86 |
| <i>Cladoselache fylleri</i> | Cincinnati Arch region, US | Mid. Devonian | scale | Wells, 44 |
| <i>Ctenacanthus clarki</i> | Cincinnati Arch region, US | Mid. Devonian | scale | Wells, 44 |
| <i>Ctenacanthus</i> sp. | Pimenteira Fm., Brazil | Mid. Devonian | fin spine | Janvier & Melo, 92 |
| | Iran | Late Givetian - Early Frasnian | | Lelievre et al., 93 |
| <i>Deirolepis carinatus</i> | Cincinnati Arch region, US | Mid. Devonian | scale | Wells, 44 |
| <i>Ellesmereia schultzei</i> | Arche Canada | Early Devonian | scales | Vieth, 80 |
| <i>Gualepis elegans</i> | Xitun Member, South China | Early Devonian | scales | Wang Nianzhong, 84 |
| <i>Hercynolepis meischneri</i> | Harz | Early Devonian | scales | Gross, 73 |
| <i>?H. meischneri</i> | Spain | Early Devonian | scale | Mader, 86 |
| <i>Iberolepis aragonensis</i> | Spain | Early Devonian | scales | Mader, 86 |
| <i>Leonodus carlsi</i> | Spain | Early Devonian | teeth | Mader, 86 |
| <i>L. cf. L. carlsi</i> | Belgium | Early Devonian | teeth | Bleick & Goujet, 91 |
| <i>Lunalepis leonensis</i> | Spain | Early Devonian | scales | Mader, 86 |
| <i>McMurdodus featherensis</i> | Aztec Siltstone, Antarctica | Givetian | teeth | Young, 91 |
| <i>Ohiolepis newberryi</i> | Cincinnati Arch region, US | Mid. Devonian | scales | Wells, 44 |
| | Ohio & Indiana, US | Early Mid. Devonian | scales | Gross, 73 |
| | Sotenich Trough, Germany | Eifelian | scales | Friman, 83 |
| | Lauch Fm., Germany | Early Eifelian | scales | Vieth-Schreiner, 83 |
| | Spain | Early Devonian | scale | Mader, 86 |
| <i>O. frohnathensis</i> | Sotenich Trough, Germany | Early Eifelian | scales | Friman, 83 |
| <i>?O. xitunensis</i> | Xitun Member, South China | Early Devonian | scales | Wang Nianzhong, 84 |
| <i>Ohiolepis</i> sp. | Heisdorf Beds, Germany & New York state, US | Emsian - Eifelian | | Orvig, 69 |
| | | | | |
| | | | | |
| | | | | |

TABLE 3. Continued.

| Taxa | Locality | Age | Material | Reference |
|-----------------------------------|--|---------------------------------|-------------------|------------------------------------|
| <i>Peilepis solida</i> | Xitun Member, South China | Early Devonian | scale | Wang Nianzhong, 84 |
| <i>Phoebodus floweri</i> | Cincinnati Arch region, US | Mid. Devonian | teeth | Wells, 44 |
| | Indiana, US | Early Mid. Devonian | teeth | Gross, 73 |
| ? <i>Ph. bryanti</i> | Cincinnati Arch region, US | Mid. Devonian | teeth | Wells, 44 |
| | Iowa, US | Early Mid. Devonian | tooth | Gross, 73 |
| <i>Polymerolepis whitei</i> | Dneister Range, Podolia | Early Devonian | scales | Orbruchev & Karatajute-Talimaa, 67 |
| | Simpson Park Range, Nevada | Lochkovian (<i>delta</i> Zone) | scales | Turner & Murphy, 88 |
| <i>Protacrodus wellsii</i> | Iowa, US | Early Devonian | scales | Gross, 73 |
| <i>Protacrodus</i> sp. | Harz & Morocco | Early Devonian | scales | Gross, 73 |
| | Germany & US | Mid. - Late Devonian | | Zangerl, 81 |
| | Iran | Late Givetian - Early Frasnian | | Lelievre et al., 93 |
| <i>Pruemolepis wellsii</i> | Lauch, Hetsdorf & Wetteldorf Fms., Germany | Emsian - Eifelian | scales | Veith - Schreiner, 83 |
| <i>Pruemolepis</i> sp. | Spain | Early Devonian | scales | Mader, 86 |
| <i>Pucapampella rodriguei</i> | Sicasica & Belen Fms., Bolivia | Eifelian | synarcual | Lelievre et al., 93 |
| <i>Zamponiopteron falciformis</i> | Sicasica & Belen Fms., Bolivia | Devonian | | Lelievre et al., 93 |
| <i>Z. triangularis</i> | Sicasica & Belen Fms., Bolivia | Devonian | fin element | Lelievre et al., 93 |
| <i>Z. spinifera</i> | Sicasica & Belen Fms., Bolivia | Devonian | | Lelievre et al., 93 |
| Possible occurrences: | | | | |
| Indet scale | Vestspitsbergen | Emsian - Eifelian | scale | Orvig, 69 |
| Pleuracanth | Bokkeveld Gp., South Africa | Late Mid. Devonian | tooth impressions | Oelofsen, 81 |
| Chondrichthyan ? | Catavi Fm., Bolivia | Late Early - Mid. Devonian | spines | Gagnier et al., 88 |
| Indet shark scale | Simpson Park Range, Nevada | Lochkovian (<i>delta</i> Zone) | scale | Turner & Murphy, 88 |
| Xenacanthid sp. nov. & others | Aztec Siltstone, Antarctica | Givetian | teeth | Young, 89; 91 |
| Chondrichthyan | Talengit sequence | Emsian | | Lelievre et al., 93 |

DESCRIPTION

Morphology. In these scales the subcircular crown extends posteriorly beyond the base such that the length of the base is approximately half to two-thirds the length of the crown (Fig. 9C,F,I,L). The parallel ridges on the crown become thinner and shallower posteriorly, and disappear at about the middle of the crown. The crown has no anterior rim; rather the ridges extend down the anterior edge of the crown and neck, ending just above the flared joint of neck area and base (Fig. 9K). The neck is shallow, in some specimens slightly deeper posteriorly (Fig. 9B,E), with only very slight

anterior and posterior indentations in lateral view. The neck area is not indented laterally. Six to ten small round neck canal openings are located in the posterior neck area (Fig. 9E). The convex base is diamond-shaped, and flared into a slight rim around the perimeter, where it connects with the neck (Fig. 9B,E,H). In some specimens the base extends anteriorly beyond the crown, producing a smooth anterior margin on the scale (Fig. 9A,D). Such scales are deeper in a dorso-ventral direction.

Histology. The conical bony base contains both fine radial fibres (Fig. 13A) and osteocytes (Fig.

13B). The crown shows no evidence of concentric growth but, like both *Gondwanalepis* and *Notolepis*, consists of apposed increments of Strangewebe-like material (Fig. 13B).

DISCUSSION

The basal view of *Aussilepis lukaso* is similar to that of the Late Silurian shark *Elegestolepis grossi* Karatajute-Talimaa, 1973 (Karatajute-Talimaa, 1973: pl. 3, figs 3b, 4b). However, the crown ornamentation of the two types of scale is quite different; the ridges on *Elegestolepis* are longer, thinner, and more numerous than those on *Aussilepis*.

Some of the scales, in lateral view, are similar to illustrated acanthodian scales, for example *Nostolepis striata* Pander, 1856 (Gross, 1947: pl. 25 fig. 7c; Denison, 1979: fig. 17f), *N. arctica* Vieth, 1980 (Vieth, 1980: pl. 5, figs 4b, 5b, 7b), *Cheiracanthoides comptus* Wells, 1944 (Gross, 1973: pl. 27, fig. 2c), or *Cheiracanthoides* sp. cf. *comptus* (Boucot et al., 1989: fig. 19a).

Apart from the absence of neck canal openings, these scales differ from *Aussilepis* in various morphological details. *Nostolepis* scales have a posteriorly pointed crown ornamented with converging ridges, commonly paired, with a median depression (Denison, 1979; Forey et al., 1992). However, the crown of *Aussilepis* scales is rounded posteriorly, and extends further beyond the base posteriorly than in the acanthodian scales. The base of *Aussilepis* is less strongly convex than the base of *Nostolepis* scales (Gross, 1947: pl. 26; Forey et al., 1992: fig. 12a).

In scales of *Cheiracanthoides comptus* Wells, 1944, the grooves between the ridges are not deep enough to notch the anterior margin (Wells, 1944). In *Notolepis* scales, the anterior edge of the crown is always deeply notched (Fig. 9K), as is also the case with *Gondwanalepis*. Scales of *C. comptus* Wells, 1944 have a constricted neck, unlike those of *Aussilepis*, and a nearly flat crown. *Aussilepis* scales have a crown that slopes down anteriorly to meet the flared rim joining the base and neck; there is no anterior rim to the crown of *Aussilepis* as there is in *Cheiracanthoides*. Scales of *C. comptus* Wells, 1944 have a 'thick, inflated' base (Wells, 1944), described by Gross (1973) as "highly domed". The base of *Aussilepis* scales is convex, but more gently so than in figured scales of *C. comptus* Wells, 1944, and appears smooth, lacking the distinct concentric striations characteristic of acanthodian scales (Gross, 1973). As with *Nostolepis striata* Pander, 1856 (Denison, 1979: fig. 17f), the crown

of *C. comptus* Wells, 1944 extends posteriorly beyond the base a shorter distance than in *Aussilepis*.

Ohiolepis Wells, 1944

TYPE SPECIES

Ohiolepis newberryi Wells, 1944

Ohiolepis sp.
(Fig. 8G-L)

REMARKS

The genus *Ohiolepis* was established by Wells (1944) for scales from the Middle Devonian bone beds of Ohio, Indiana, and Kentucky. His two species, *O. newberryi* and *O. stewartae*, were subsequently united by Gross (1973), who ascribed differences in shape between the two species to scales coming from different parts of the body. The taxon has also been reported from Australia (Schultze, 1968; Giffin, 1980; Turner, 1982; Pickett et al., 1985; Turner, 1993; Young, 1993), China (Wang, 1984), and Germany (Ørvig, 1969; Friman, 1983; Vieth-Schreiner, 1983); see Tables 2, 3. Turner (1993) questioned the chondrichthyan affinities of some of these records, suggesting that some might be placoderm scales.

Two new species have been erected since Gross's 1973 amalgamation: '*Ohiolepis*' *frohnathensis* Friman, 1983 from the early Eifelian of Germany, and *O. ? xitunensis* Wang, 1984 from the Early Devonian of China. All other occurrences have been assigned either to *O. newberryi* or simply to the genus.

Scales assigned to the genus and figured in the literature vary in morphology. Wells (1944) established as generic characters a flat or convex base; a broad crown ornamented by numerous spines that are enamelled, anteriorly indented or grooved, with an anterior sloping face, acute posteriorly inclined tips, and resting directly on the base; and a narrow, spine-free strip around the anterior edges and sides of the scale. However, Wells (1944:38) also remarked that the spines of *O. newberryi* Wells, 1944 may be blunt and club-shaped; this is inconsistent with his diagnosis. Wells described his less common second species, *O. stewartae*, as having spines similar to those of *O. newberryi* Wells, 1944, but fewer in number, and arranged in a single transverse series with the smallest spine in the centre.

Gross (1973) placed the two species in *O. newberryi* Wells, 1944 by combining Wells's two

groups of specific characters, but made no mention of the spines being blunt or club-shaped, or having an anterior groove. However, his illustrations show scales with both pointed (Gross, 1973: pl. 30, figs 8-21) and blunt-tipped (pl. 31, fig. 8) spines, and both with (pl. 30, figs 8-21) or without (pl. 31, figs 6,7) an anterior groove. Most of Gross's figures (1973: pl. 30, figs 8-19,21; pl. 31, figs 3-7) show examples similar to Wells's original *O. newberryi* type, with numerous closely-packed spines, each having an anterior groove and a posteriorly-directed acute tip. Other examples (Gross, 1973: pl. 31, figs 1, 2) have the spines more widely-spaced and conform more closely to Wells's original description for *O. stewartae*. Indeed, all specimens of *Ohiolepis* described since 1973 have widely-spaced spines (Giffin, 1980: fig. 4a,b; Friman, 1983: figs 1,2; Vieth-Schreiner, 1983: pl. 4, fig. 36; Wang, 1984: figs 16,17; Pickett et al., 1985: cover photo K). On this evidence, it seems best for the moment to provisionally retain Wells's two species, with *O. newberryi* only known from North America, and examples from elsewhere showing more resemblance to *O. stewartae*. In the absence of precise locality data, it is possible that the material analysed by Gross came from several different horizons.

The concept of the genus *Ohiolepis* is further confused because one of Friman's (1983) species characters for '*Ohiolepis*' *frohnathensis* is inconsistent with Wells's (1944) genus diagnosis: '*Ohiolepis*' *frohnathensis* Friman, 1983 scales lack an anterior groove on the spines. One option is to consider anterior grooves on the spines a generic character applying to most scales in a sample, but accepting some variation in scales from different regions of the body. Friman's specimens (1983: fig. 2b-c) have spines on the crown not dissimilar to those found on dermal denticles from the branchial region of *Antarctilamna prisca* Young, 1982 (fig. 2c,d; pl. 87,

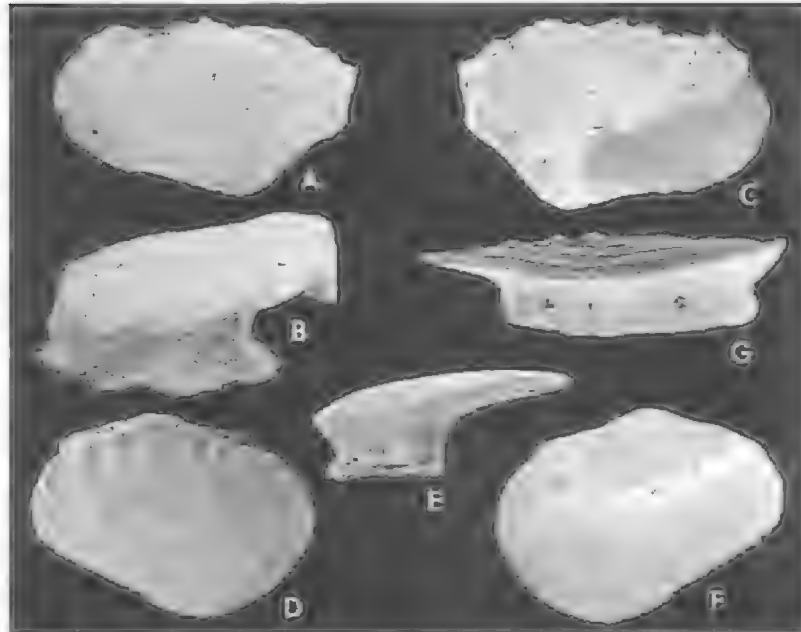


FIG. 10. A-C, Chondrichthyan A - fam., gen. et sp. indet., scale QMF26110 from SD15/192; D-G, Chondrichthyan B - fam., gen. et sp. indet., scale QMF26111 from SD204/174. A, crown view, x 32; B, lateral view, x 56; C, basal view, x 32; D, crown view, x 48; E, lateral view, x 72; F, basal view, x 48; G, posterior view, x 68.

figs 9,10), so this morphotype might occur in many different shark taxa.

Wang's (1984) *O. ? xitunensis* was provisionally referred to *Ohiolepis*. Listed differences between *O. newberryi* Wells, 1944 and his new species included shape of the denticles, and shape and structure of the base.

MATERIAL

Six scales; QMF26103-5, QMF31828-30 (Fig. 8G M).

LOCALITY AND HORIZON

The scales occur in four sections of the Broken River Group (SD128, SD130, SD204 and SD216 - Fig. 2), in horizons of the Papilio Formation and the associated Spanner Limestone Member aged middle and upper *varcus* Conodont Zone. This age is younger than other occurrences of *Ohiolepis*; both Ørvig (1969) and Friman (1983) consider the genus to be characteristic of Emilian/Eifelian boundary beds in Europe, North America, and Australia.

MEASUREMENTS

The scales range in length from 0.7mm to 2.5mm, and in width from 0.7mm to 1.6mm.

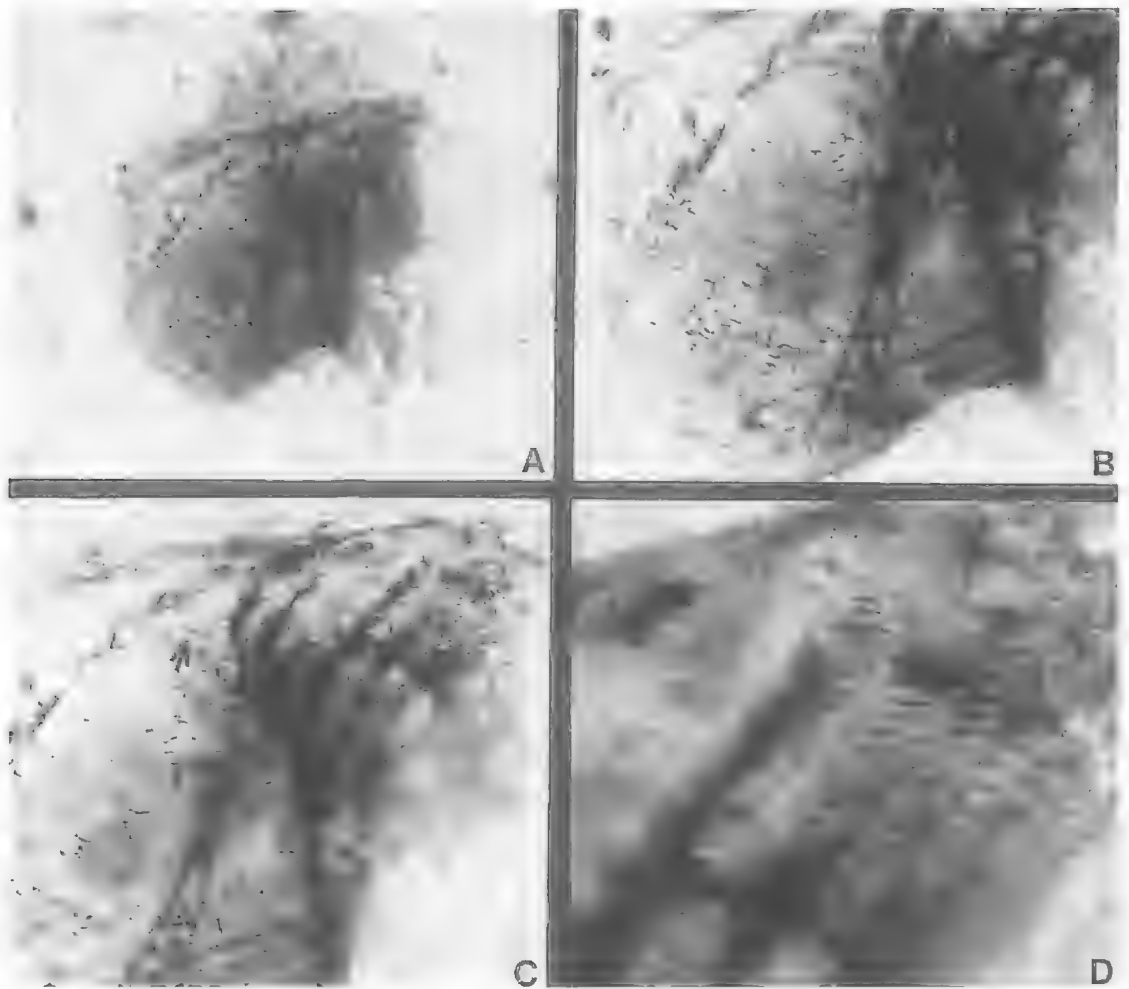


FIG. 11. *Gondwanalepis grossi* gen. et sp. nov., longitudinal section QMF26112 of scale from SD204/174 upslope. A, full view, x 30; B, detail of base, x 60; C, detail of posterior part of scale, x 60; D, detail of posterior part of crown, x 180.

DESCRIPTION AND DISCUSSION

With only six scales, the examples from Broken River can only be provisionally compared with *Ohiolepis*. Each has a crown completely covered with numerous small, conical, closely-packed, posteriorly inclined tubercles or spines, without an anterior groove (Fig. 8G,I,J,K,M). The spines radiate from the centre anterior margin (Fig. 8G,M) and cover the crown, although one specimen (Fig. 8M) has a small spine-free area in the central anterior region of the crown. Broken spines (arrows in Fig. 8M) show a central cavity. The scales have a subcircular to subrectangular outline, a very shallow neck, and a flat or slightly concave unornamented base (Fig. 8H).

The crown of these new scales has spines finer and more closely-packed than those in the illustrations of *Ohiolepis* by Gross (1973), Giffin (1980), Friman (1983), Vieth-Schreiner (1983), Pickett et al. (1985), and ?*Ohiolepis*-type scales of Liszkowski & Racki (1993). However, one illustration by Wells (1944: fig. 7f) shows small, closely-packed spines, similar to the Broken River specimens. The spines of the Broken River scales overlap (Fig. 8J,M), in contrast to the condition noted by Gross (1973).

The profile of the scales is low and flat, similar to Giffin's (1980) description of the *Ohiolepis* scales from Taemas. Gross (1973) commented that it is hard to differentiate between the crown

and the neck; this is the case with the Broken River scales.

The spines have a round or oval cross-section, without an anterior groove, thus resembling Friman's (1983) species '*Ohiolepis*' *frohnrahtensis*, as discussed above.

Friman (1983) described the ornamentation of '*Ohiolepis*' *frohnrahtensis* as asymmetrical, but according to Gross (1973), the spines on the crown are arranged both concentrically and in diagonal rows, with the earliest formed, smallest spines located in the centre, and later ones added around the edges. In most illustrated specimens in the literature, the spines appear to be approximately symmetrical, subparallel and pointing posteriorly; this is also the case in the Broken River specimens.

The Broken River scales have a subcircular to subrectangular outline, and a flat or slightly concave base. According to Wells (1944), the base of *O. newberryi* may be flat or convex. The base of '*Ohiolepis*' *frohnrahtensis* Friman, 1983 is always anteriorly convex (Friman, 1983), while that of *O. ? xitunensis* Wang, 1984 is flat (Wang, 1984).

Cladolepis Wells 1944

TYPE SPECIES

Cladolepis gunnelli Wells, 1944

Cladolepis sp. cf. *C. gunnelli*
(Fig. 7K-M)

Cladolepis gunnelli Wells 1944: 36,37; pl. 3, figs. 2-7; pl. 8, fig. 4; fig. 6a,b,d.

Cladolepis ornata Wells 1944: fig. 6h.

Cladolepis sp. Wells 1944: fig. 6c,i.

Cladolepis gunnelli Gross 1973: 97-99; pl. 31, figs. 11-17; pl. 32, figs. 1,2.

?*Cladolepis gunnelli* Gross 1973: pl. 31, figs. 9,10.

Cladolepis ? gunnelli Vieth-Schreiner 1983: 151,152; pl. 3, fig. 25.

Cladolepis cf. *gunnelli* Mader 1986: pl. 7, fig. 10.

REMARKS

Cladolepis was erected by Wells (1944) from material from the bone beds of the Cincinnati Arch Region, from horizons subsequently dated by conodonts as *kockelianus* Zone or older (Klapper & Johnson, 1980). The Broken River scales resemble *Cladolepis gunnelli* Wells, 1944 in shape and crown ornamentation, but differ in having a thick, sloping crown rather than the flat thin crown of *C. gunnelli* Wells, 1944. The base

is 'convex and acanthodianlike', as Wells (1944) described some of his specimens. The crown ornamentation is also similar to that of *Antarctilamna prisca* Young, 1982, but that form has a completely different base.

MATERIAL

Seven scales - one intact (QMF26100), three broken at posterior, three severely broken or abraded.

LOCALITY AND HORIZON

The scales occurred in three sections (SD190, SD192, SD210) from horizons of the Papilio Formation and the Stanley Limestone Member of the Mytton Formation, dated middle and upper *varcus*, *hermanni-cristatus* and *asymmetricus* conodont zones.

MEASUREMENTS

The only unbroken scale (QMF26100) measures 1.9mm long, 2.2mm wide and 0.7mm high. All other specimens have the posterior section broken.

DESCRIPTION

The rounded rhombic or subdiamond-shaped crown slopes gently up from the anterior and flattens out towards the posterior (Fig. 7L). The posterior margin is slightly pointed. The crown is covered in curved, concentric low ridges that parallel the lateral margins of the scale, and converge posteriorly. The central anterior part of the crown has short, curved, overlapping ridges; these short central anterior ridges and the anterior part of the longer side ridges are grooved (Fig. 7K). The neck area is shallow to nonexistent, and is not indented. The base is diamond-shaped and gently convex (Fig. 7L,M). The anterior part of the base extends beyond the crown, producing a flat, unornamented rim along the anterolateral margins of the scale (Fig. 7K). The crown overhangs the base posteriorly. Where the base joins onto the neck area, a rim is formed, especially at the posterior (arrow in Fig. 7L).

DISCUSSION

The crown ornamentation resembles that of *Antarctilamna prisca* Young, 1982 with concentric ridges converging posteriorly, and grooves on the anterior part of the ridges. The Broken River scales differ from those of *A. prisca* Young, 1982 by having a large, diamond-shaped, convex base and shallow, broad neck; *A. prisca* Young, 1982 scales have a deeply concave, cup-shaped base and a constricted neck

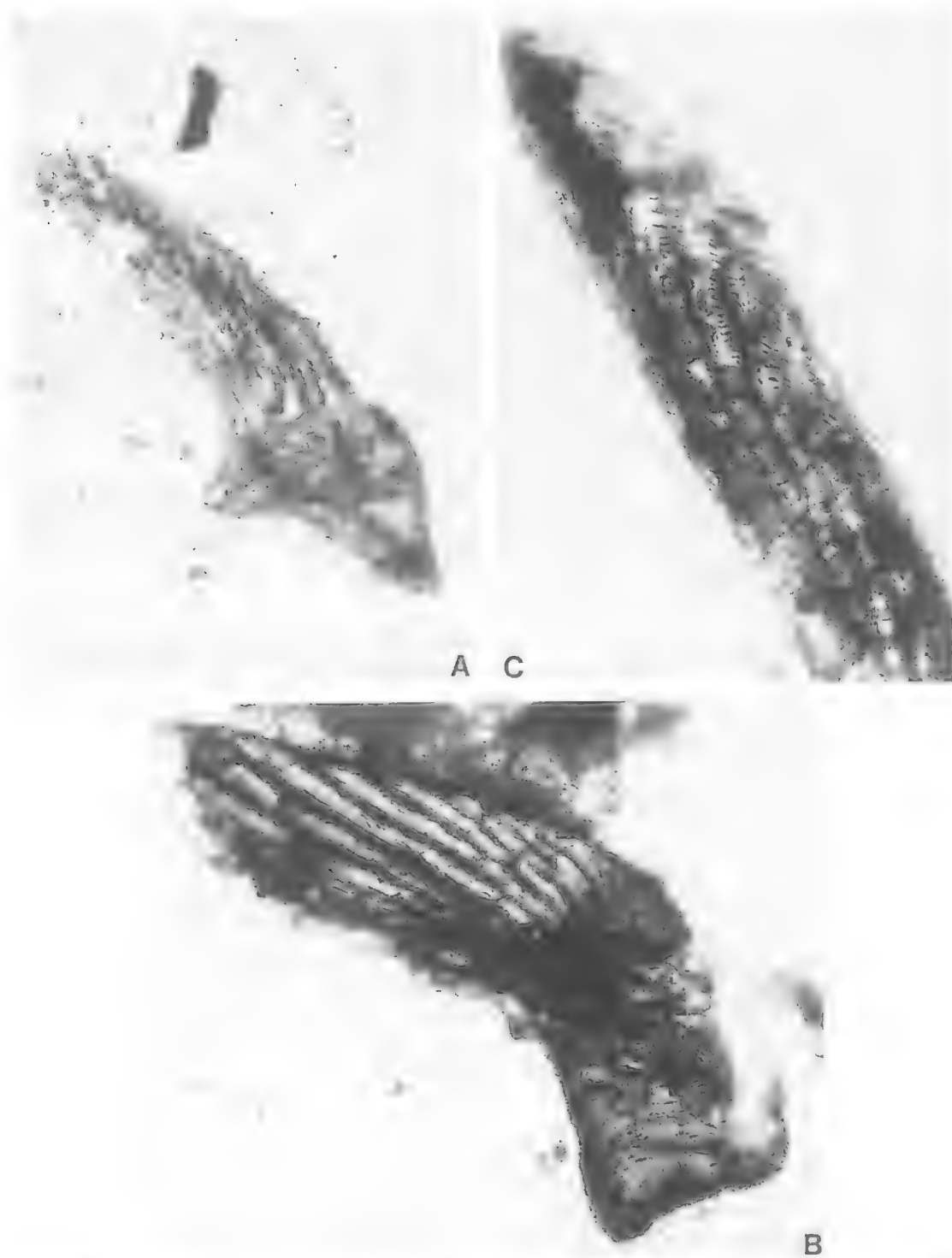


FIG. 12. *Notiolepis dienemos* gen. et sp. nov., SD204/174 upslope. A, longitudinal section QMF31912 of scale, x 45; B, longitudinal section QMF 31913 of scale, x 45; C, longitudinal section QMF31914, detail of posterior part of crown, x 90.

(Young, 1982). The Broken River scales also possess several short, flat, curved ridges in the central anterior section of the crown. Such ridges are absent in some scales of *A. prisca* figured by Young (1982: pl. 87, fig. 7; text-figs 2b, 4d); however, one illustrated scale (Young, 1982: pl. 87, fig. 6) shows two short anterior ridges, similar to those present in *Cladolepis*. Enlarged photographs of the holotype of *A. prisca* Young, 1982 show several scales in the dorsal fin area with the short, overlapping, grooved anterior ridges characteristic of *Cladolepis* scales, so this type of scale variation can occur on different parts of the body. Scales referred to *Antarctilamna* sp. by Forey et al. (1992) from the Pragian or early Emsian of Saudi Arabia have superficially similar crown ornamentation to the Broken River specimens. They differ from both the Broken River and *A. prisca* Young, 1982 scales in having finer ornamentation, a larger number of the shorter anterior ridges, and by having the anterior area of shorter, flatter ridges more clearly delineated from the rest of the crown. The scales from both Broken River and Saudi Arabia are a similar size, approximately 2mm; this is slightly larger than the *A. prisca* Young, 1982 scales from Antarctica.

The thick, convex base of the Broken River specimens is similar to that of *Ohiolepis newberryi* Wells, 1944 and *Protacrodus wellsi* Gross, 1973, but the crown ornamentation is different.

Scales from a possible species of *Cladolepis* have been reported from the *gigas* Zone Mouty Vale Formation near Keepit, NSW (Turner, 1993). Overseas, the genus is known from the early Eifelian Lauch Formation of the Wollenbach member (Vieth-Schreiner, 1983), the Middle Devonian of Indiana (Gross, 1973), the Cincinnati arch region (Wells, 1944), and the middle Givetian to early Eifelian Holy Cross Mountains of Poland (Liszkowski & Racki, 1993). Cladodont teeth are known in Australia, including the Broken River area (Turner, 1982), from Late Devonian and younger horizons.

Chondrichthyan A - fam., gen. et sp. indet.
(Fig. 10A-C)

MATERIAL

Figured scale QMF 26110 and two other scales.

LOCALITY AND HORIZON

Scale QMF26110 is from section SD15, in the middle *varcus* Conodont Zone Papilio Formation. The other scales occurred in the Papilio Formation of section SD131, dated middle *varcus* Conodont Zone, and the Spanner Limestone of section SD216, dated *hermanni-cristatus* Conodont Zone.

REMARKS

This chondrichthyan scale is not similar to any described form. An unusual feature is a thickened central ridge on the underside of the posterior section of the crown. Examination of more specimens will be required before the scales can be confidently assigned to a genus.

MEASUREMENTS

The scales measure 0.4mm to 0.75mm in length, 0.65mm to 1.2mm in width, and 0.2mm to 0.4mm in height. The length is approximately twice the height, and the width is approximately three times the height.

DESCRIPTION

The crown is wider than long, and slopes up towards the posterior margin. The crown is gently curved at the front, and more pointed at the back. The anterior half of the crown has approximately 12-14 shallow, subparallel ridges, not clearly defined (Fig. 10A). Two or three narrow, low, closely-spaced ridges parallel the posterior margins of the crown. The neck is shallow at the anterior, deeper and clearly indented at the posterior (Fig. 10B). The subtriangular base is flat or gently concave and flared into a thin trim around the edges (Fig. 10B,C), and, like the crown, is wider than it is long.

Chondrichthyan B - fam., gen. et sp. indet.
(Fig. 10D-G)

MATERIAL

Figured scale QMF26111 and four other scales.

LOCALITY AND HORIZON

The scales occurred in three sections (SD128, SD204 and SD210 - Fig. 2), in horizons of middle *varcus* Conodont Zone age.

REMARKS

The anterior rim and ridges on the crown are similar to those found on scales of the acanthodian *Cheiracanthoides comptus* Wells, 1944 (e.g. Vieth-Schreiner: 1983, pl. 4, fig. 32). How-

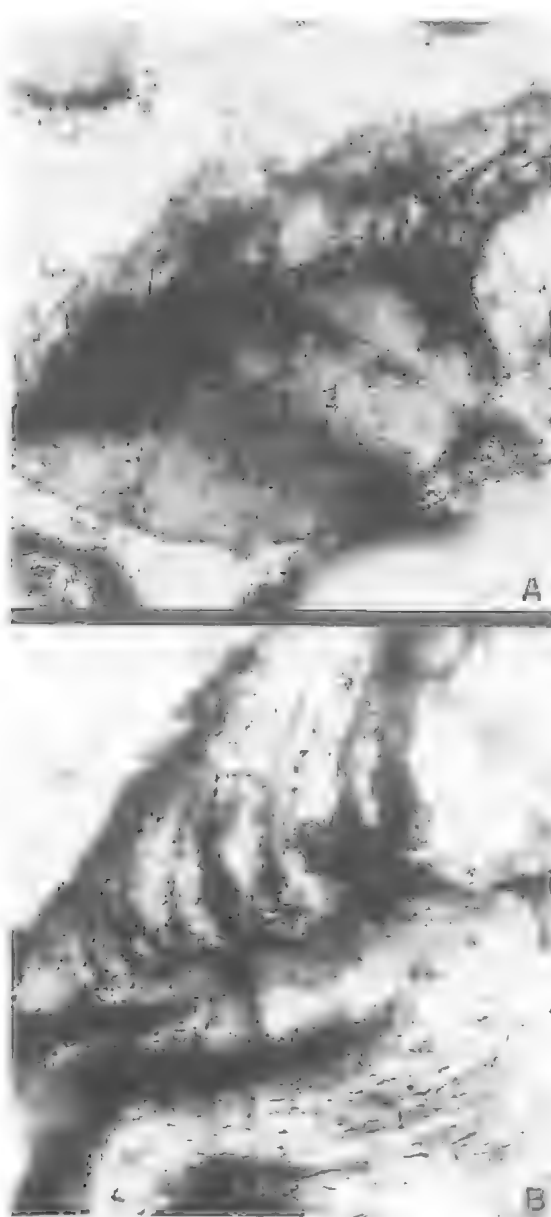


FIG. 13. *Aussilepis lukaso* gen. et sp. nov., SD204/174 upslope. A, longitudinal section QMF26113 of scale showing base and central part of crown, x 60; B, longitudinal section QMF26114, detail of posterior part of scale, showing base and crown, x 80.

ever, these scales from Broken River do not have the shallow neck and deep rounded base typical of acanthodian scales (Turner, 1991). Rather, they have neck canal openings, a relatively high neck, and a flat, diamond-shaped base, distinctive

of shark scales (Turner, 1991; Turner & Young, 1987).

MEASUREMENTS

Dimensions of the one intact scale are length 0.6mm, width 0.8mm, and height 0.15mm.

DESCRIPTION

The crown is oval-shaped, thin, and flat (Fig. 10D-G). Seven subparallel ridges extend from the rim at the anterior edge to approximately halfway along the scale; the outer ridges extend into concentric ridges parallel to the posterior margin of the scale (Fig. 10D). The neck is fairly deep, not indented, and has circular canal openings around the posterior edge (Fig. 10G). The base is a narrow diamond shape, elongated across the width of the scale, and is flat (Fig. 10F).

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THE USE OF SPIDER SILK IN THE INITIATION OF NEST-BUILDING BY WEAVER ANTS (FORMICIDAE: FORMICINAE: POLYRHACHIS)

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Dwyer, P.D. & Ebert, D.P. 1994 1201: The use of spider silk in the initiation of nest-building by weaver ants (Formicidae: Formicinae: *Polyrhachis*). *Memoirs of the Queensland Museum* 37(1): 115-119. Brisbane. ISSN 0079-8835.

Field and laboratory observations of *Polyrhachis doddi* and *P. pilosa* in southeastern Queensland, Australia, showed that spider silk is used commonly in nest-building, is used often instead of larval silk when workers initiate nests or extend pre-existing nests and, at least in the laboratory when larvae are unavailable, may be used to build entire nests. Founding queens of both species also used silk from spiders when initiating nests. In nearly all cases, silk came from shelters of spiders such as salticids and clubionids. Silk from spider webs was rarely used. The functional and evolutionary significance of the use of spider silk are discussed. □ *Polyrhachis*, weaver ants, nest-building, spider silk, founding queens.

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Many species of the Old World formicine genus *Polyrhachis* use silk that is produced by their own larvae in the construction of nests (Hölldobler & Wilson, 1983, 1990). This behaviour is particularly evident in arboreal species of several subgenera (e.g. *Cyrtomyrma*, *Myrmatopa*, *Myrmhopla*) which build pocket nests of silk on tree trunks and the undersides of leaves or which use silk to join the leaves of various trees and shrubs (Dorow & Maschwitz, 1990; Dorow et al., 1990; Kohout & Taylor, 1990; Ofer, 1970; Yamauchi et al., 1987). In nests of the latter kind, as made by Australian *Cyrtomyrma* species for example, interior walls are covered by a thin, tough layer of silk and exterior portions, joining leaves, may be strongly reinforced by debris. At completed nests, neither the larval silk nor the ants inside are visible.

Nest-weaving, as described in *Polyrhachis* species and in other weaver ants, poses two related problems which have not received attention. First, in the earliest phase of colony formation, queens do not have larvae and, hence, lack access to larval silk with which to initiate nests. Secondly, initiation of new nests by workers requires transport of larvae from sheltered sites to open situations where they may be exposed to both potential predators and exigencies of weather. One of us, for example, has observed substantial predation by the skink *Lampropholis delicata* upon *Polyrhachis* larvae during a mass movement from one arboreal nest to another. The skinks attempted to retrieve larvae from *Polyrhachis* workers while avoiding direct contact with the workers themselves. Chemicals released

by the ants are a powerful deterrent to these lizards (cf. Bellas & Hölldobler, 1985).

In the green tree ant, *Oecophylla*, founding queens do not make nests; these ants are cryptically coloured and they rest, and commence rearing their first broods, in exposed positions on the undersides of leaves (Dorow et al., 1990; Peeters & Anderson, 1989; Wheeler, 1915). Again, when *Oecophylla* workers initiate nests, the security of exposed larvae is ensured firstly by the recruitment of many workers that may defend those larvae and, secondly, by the rapidity with which nests may be built (Hölldobler & Wilson, 1990). Neither of these options is available to species of *Polyrhachis* (*Cyrtomyrma*) which are black and conspicuous and do not recruit large numbers of workers to new nest sites. In this paper we report that, in two Australian *Cyrtomyrma*, a common solution to potential problems associated with initiating nests entails the use of silk produced by spiders as a substitute for that produced by ant larvae. The use of alternative silks by these weaver ants has not previously been recognised. Indeed, Dorow et al. (1990: 184) wrote that, in the laboratory, the Southeast Asian *P. muelleri* did not accept silk from spider webs. Our observations have significance for both functional and evolutionary interpretations of weaving behaviour in *Polyrhachis*.

STUDY AREA AND METHODS

In southeastern Queensland, *P. doddi* and *P. pilosa* are abundant species of arboreal weaver ant. Both make nests in many different species of plants of diverse leaf form. For example, 60 nests

of these species censused in May 1993 at the Mt Coot-tha Botanic Gardens, Brisbane, were located in 30 plants of 23 species in 10 families (17 nests in Myrtaceae, 16 in Arecaceae and 12 in Theaceae; C. Hunter, pers. comm.). Nests of these species are also found, among other places, in hollows of dead *Plumeria* branches, leaf bases of bromeliads, petioles of climbing *Philodendron*, rolls of *Eucalyptus* bark and a variety of artificial sites (e.g. plastic buckets and covered plant pots suspended in trees).

From January 1993 to February 1994 we made opportunistic observations of nest-building by *P. doddi* and *P. pilosa* in suburban gardens, and at the St. Lucia campus of the University of Queensland, Brisbane. From September 1993 to February 1994 we also made observations of nest-building by captive *P. doddi*. Groups of 25 to 55 workers were established in 28 × 21 × 7 cm plastic trays that were isolated by moats. (In the field *P. doddi* and *P. pilosa* initiate nests using groups of less than 20 workers). The trays were weighted with sand, sticks were provided as walkways and plant debris (very small leaves and broken seed capsules of *Melaleuca* and *Lepidospermum*) was supplied. Each tray was provided with a small artificial tree, less than or equal to 30 cm high, consisting of two or three branches of 'silk' (rayon) Ficus. Artificial trees were made in such a way that parts of some leaves of different branches were 0.5–1.0 cm apart but not in contact. Leaves were aligned more or less vertically. Fibres from the 'silk' plants were not used in construction of nests. Sampled nests were from *Buckinghamia celsissima* and *Casuarina littoralis*. Ants were fed on a mixture of egg and honey according to the recipe in Hölldobler & Wilson (1990: 632). All observations were at temperatures between about 15 and 30°C.

RESULTS

FIELD OBSERVATIONS

Spider silk is often visible in the walls of new *P. pilosa* and *P. doddi* nests before these walls are covered with debris. Spider silk is sometimes included with plant fragments, insect frass and fragments of chitin as part of the outer, protective cover of nests. Workers of both species have been seen harvesting silk from shelters built by spiders and transporting it to nest sites. In the field, we have not seen larvae being used in open situations during the earliest phase of nest-building.

P. pilosa have been observed to initiate nests without the aid of larvae on at least six occasions.

These nests were made in or between leaves of *Syzygium luehmannii*, *Backhousia citriodora*, *Howea forsteriana*, *Mangifera indica*, *Caryota mitis* and *Brachychiton acerifolium*. In the first three cases, 10 to 20 ants used silk from shelters of unidentified spiders; they worked for two to four days to provide partially enclosed spaces before carrying larvae to the nest sites. The fourth nest was initiated, but not completed, in a dead, furled leaf of *Mangifera indica* caught in the abandoned web of a *Nephila* (Araneae). Ants manipulated the web to increase leaf curvature and attached debris to strands of web that joined the edges of the leaf. After three days, when a partial shelter had been formed, one larva was carried to the new nest. The fifth nest, built by a founding queen, was in a rolled leaflet of *Caryota mitis*; this leaflet had originally housed a spider shelter and silk from the shelter, together with a little attached debris, formed the exposed walls of the nest. The sixth nest was initiated by *P. pilosa* workers that used waxy filaments secreted by a coccid (Homoptera) to join the leaves.

Sites chosen for building nests in two large stands of *Phoenix roebelenii*, one stand occupied by each species of *Polyrhachis*, contained shelters of salticid and clubionid spiders, including those of *Opisthoncus* and *Clubiona*. These spider shelters were spun between adjoining leaflets of fronds and, particularly with the tightly woven shelters of salticids, had the outcome that the leaflets were pulled together and overlapped for part of their length. *Polyrhachis* workers with larvae cannot achieve this rearrangement of the thick, stiff leaflets (personal observations). Because the orientation of leaflets at nearly all *Polyrhachis* nests in these palms matched the orientation produced by spiders we think that most observed nests ($n = 12$) were initiated at spider shelters. At one *P. doddi* nest the 16 cm long walls that joined two leaflets were made entirely of silk from the shelters of spiders. Workers were seen harvesting silk from a nearby salticid shelter and carrying it to the nest.

Two large, galleried nests of *P. doddi* in *Casuarina cristata* and one small nest in *Syzygium luehmannii* were extended by workers that carried silk from spider shelters to the sites; larvae were not used until the extensions were well underway and provided covered areas within which workers could effectively hide the larvae from view. Four nest sites used by founding queens of *P. doddi* were established at spider shelters in furled leaves of *Tupidanthus calyptratis* and *Schefflera actinophylla*. The

queens had teased apart the spider shelters and attached some debris to make open nests that, in two cases, were used for more than a month by up to eight queens. Founding queens of *P. doddi* have been often observed sheltering under or inside palm leaflets which had been either folded by spiders making silk shelters or rolled by the larvae of palmdarts (*Cephenes*). In the latter case, abandoned *Cephenes* shelters that had subsequently been used by spiders were preferred by the queen ants. When using temporary shelters during the daytime, *P. doddi* queens are often in contact with the silk of spider shelters, either between leaves or in leaves that have been curled by the spiders.

LABORATORY OBSERVATIONS

In mid-September 1993, three groups of workers, each with access to an artificial tree, were provided with silk from old, abandoned salticid and clubionid shelters. Three additional groups were provided, respectively, with spider web and egg cases (the latter from *Zosis* sp. [Uloboridae: Araneae]), cotton wool and five large larvae. All groups, except that with cotton wool, initiated nest-building in late September and continued intermittently through October and November. In late November the group with larvae and two of the groups with salticid and clubionid shelters had completed building nests between leaves of the artificial trees. After several aborted attempts, the group with web and *Zosis* egg cases used silk from the egg cases to complete a small nest beneath a stick on the floor of the tray.

On December 24, 1993, three groups of workers in artificial trees were provided with silk from recently built salticid and clubionid shelters. On February 8, 1994, these groups of ants had completed two-thirds, one-quarter and one half, respectively, of the areas of wall needed to enclose each nest. The trial was then terminated because, in two groups, larvae produced by workers were approaching the size at which they might produce silk.

Donor colonies of *P. doddi*, housed in the laboratory, also built nests using silk from salticid and clubionid shelters. These large groups, with queens and larvae, initiated nests with spider silk more often than with larval silk. One group took apart, and reused, the entirety of an old nest; in another group, with about 200 workers, ants began harvesting spider silk 10 minutes after the silk was provided.

In the laboratory, *P. doddi* workers harvested silk from spider shelters by tearing at the shelter and pulling and biting portions free. They did not cooperate in this activity. Often, however, when the load had been carried to the nest site it was attached to an artificial leaf at places which had been moistened by fluid from the mouth of another worker. Sometimes the ant that carried the spider silk waited as the other ant moistened the leaf and, on a few occasions, the latter ant retrieved the silk from the former and attached it to the leaf. This behaviour differs from that of *Polyrhachis muelleri* which, when using old larval silk or cotton wool, glued the material into place with a droplet from the tip of the gaster (Dorow et al., 1990).

P. doddi seldom isolated single fibres from the masses of spider silk that were transported to nest sites. They teased each load apart to produce a flocculent mass of fibres. These were either built out from one leaf surface in layers or stretched between two leaves by manipulating with mandibles and anterior legs. Plant debris was inserted into the mesh of fibres rather than being stuck onto it as occurs when larval silk is used. In two cases, when a vertical wall was built from spider silk the weight of attached debris contributed to pulling silk fibres from the upper to the lower leaf edge. In the laboratory, all *P. doddi* nests built between vertically aligned leaves were commenced at the bottom, proceeded through arching, vertical walls and were completed by covering the top of the chamber and making an entrance. Nests made in analogous situations in the field were also built in this sequence.

Nests made entirely from spider silk were not as strong as those that incorporated larval silk. The latter material provides a firm base to which debris can be attached with some precision. Walls constructed from spider silk lack rigidity and cannot support a complete cover of plant debris without collapsing. Nor can workers construct the characteristic well-formed circular entrance to the nest without access to larvae. The quality of laboratory built nests, made from spider silk alone, is such that they would fall apart rapidly if exposed to even moderate rain or wind.

DISCUSSION

Field and laboratory observations of *P. doddi* and *P. pilosa* show that silk produced by spiders is used very commonly in nest-building, is used often instead of larval silk when workers initiate nests or extend pre-existing nests and, at least in

laboratory settings, may be used to build entire nests. In all these cases, *Polyrhachis* workers actually manipulated or transported spider silk in the process of nest-building. We are not dealing merely with the use of 'preformed shelters of spiders and caterpillars' which Maschwitz et al. (1991: 308) reported for an arboreal dolichoderine ant (*Technomyrmex* sp.); they commented that sites of these kinds might be easily 'misidentified as nests produced by the ants themselves'. Founding queens of both *P. doddi* and *P. pilosa* have been also observed to use silk from spiders when initiating nests. Indeed, there appears to be a close association between *P. doddi* queens and abandoned spider shelters.

Our observations suggest that silk from spider shelters is much more likely to be used by *P. doddi* and *P. pilosa* than silk from spider webs. Nests of these species are, however, often built where leaves are tangled in web and we have sometimes seen *P. pilosa* tugging at and manipulating silk in webs that were occupied by spiders. Dorow et al. (1990) reported that 'silk from spider webs' was not accepted by nest-building *P. muelleri*; it is possible, however, that this species would accept other forms of spider silk.

Arboreal *Polyrhachis* species do not display the highly cooperative nest-building behaviour seen in *Oecophylla* where large numbers of ants, recruited to favourable sites, form lines or hanging chains and bend or manoeuvre leaves such that larval silk can be used to hold those leaves in their new positions (Hölldobler & Wilson, 1977, 1990). Rearrangement of leaves observed at many arboreal nests of both *P. doddi* and *P. pilosa*, especially in stiff-leaved plants (e.g. some palms), could not be achieved by the ants themselves, either with or without assistance from larvae. Most of these nests will have been initiated at places where leaves had been already repositioned through the actions of other animals, usually by spiders spinning silk shelters. By contrast, in various Myrmecae species, *Polyrhachis* workers preferentially build nests in young leaves which are easily bent into unconventional positions; even in these plants, however, our observations were only of nests initiated or extended using spider silk and not larval silk. Dorow & Maschwitz (1990) described rapid recruitment of *P. hodgsoni* workers and larvae to potential nest sites on broad-leaved bamboo (*Gigantochloa* and *Schizostachyum*); ants opportunistically exploited occasions when changes in turgor caused

edges of a leaf to move towards each other. These authors also reported that nests of *P. hodgsoni* were also built in leaves that had been rolled by spiders, orthopterans, caterpillars and climbing plants. At exposed sites, where larvae would be easily visible, *P. doddi* and *P. pilosa* usually commence nest-building without recruiting larvae to the site.

With specific reference to *Oecophylla*, Hölldobler & Wilson (1990: 618) argued that weaving behaviour freed ants from 'the spatial limitations imposed on species that must live in beetle's burrows, leaf axils ... and other preformed vegetation cavities' (see also Dorow et al., 1990, on *Polyrhachis* and Maschwitz et al., 1991, on *Dolichoderus*). Dorow et al. (1990: 188) commented further that in arboreal *Polyrhachis*, as in *Oecophylla*, weaving behaviour facilitates polydomy which, itself, may be beneficial in reducing distances to food sources, providing alternative nest sites after catastrophes and, perhaps, facilitating defence of foraging areas. Observations reported here both reinforce and extend earlier conclusions. Use of spider silk as an alternative to larval silk will increase the availability of nest-building sites to *P. doddi* and *P. pilosa* and allow assessment of the quality of potential nest and foraging sites by workers prior to incurring the costs of transporting larvae. Potential costs to larvae that would arise from silk production and risks associated with exposure will be also reduced when silk from spiders is used to initiate nests. And, further, our observations show how founding queens, which lack access to larval silk, may initiate arboreal nests.

Hölldobler & Wilson (1990) considered that the exploitation of larval silk by workers released weaver ants from their ancestral dependence upon a variety of preformed vegetation cavities. This opinion is difficult to accept if, as Dorow et al. (1990) suggested and our observations imply, the failure of *Cyrtomyrma* species to make cocoons is independent of the amount of silk contributed to nest-building. The behaviour of both workers and founding queens of *P. doddi* and *P. pilosa* suggests that use of spider silk could have been a precursor to use of larval silk in the origin of nest-building by at least some groups of arboreal *Polyrhachis*. Answers to questions regarding the origins of these behaviours will require comparative knowledge of silk production in the genus as a whole and knowledge of the extent to which silk production is under worker or larva control.

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NEW CONSERVATION STATUS FOR ANOMALOPUS PLUTO (SCINCIDAE). *Memoirs of the Queensland Museum* 37(1):120. 1994 :- Recently (17 May 1994) the authors collected three specimens of *Anomalopus pluto* on the Glennie Tableland (13°27'S 142°58'E), FNQ.

Two were found at 260m, under sandstone slabs on a narrow, flat sandstone ridge, in dark sandy loam and humus. This is an area of dense shrubland with low, windswept trees. The third (collected 18 May, 1994) was found under a rotting log in a patch of monsoon vine forest in the same soil, at the same altitude. These specimens were photographed and released. Copies of the photographs have been lodged in the Queensland Museum photographic index (NP 79-83).

These specimens extend the range of this species almost 200km south. Couper (1992) reviewed the range and status of *A. pluto* following its collection in the Heathlands area (11°45' 142°35'). He treated it as a '2K' species under the conservation status definitions used by McDonald et al., 1991. That is, as a species '... with a very restricted distribution ... and with a maximum geographic distribution of less than 100km ...'; poorly known ... accurate field distribution information ... inadequate'.

Discovery of *A. pluto* on the Glennie Tableland changes its conservation status to '3K': '... with a range greater than 100km ... but occurring in small populations which are mainly restricted to highly specific habitats; poorly known ...'.

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- T.A. Hawkes, P.J. Lethbridge, M. Anthony & M. McGregor, *Cape York Herpetological Society, PO Box 114, Palm Cove (Cairns), Queensland 4879, Australia; 30 September 1994.*

NEW DATA ON THE DISTRIBUTION OF PYGOPUS LEPIDOPODUS (PYGOPODIDAE). *Memoirs of the Queensland Museum* 37(1):120. 1994:- That *Pygopus lepidopodus* occurred north of the Yeppoon area, MEQ (23°08'S 150°44'E) was unknown until 1991. Ingram & Raven (1991) noted its occurrence at Yungaburra (QMJ3899, 17°16'S 145°35'E) and Shipton's Flat (QMJ47145, 15°48'S 145°15'E), NEQ.

Two more specimens have been recorded recently, on northern Cape York Peninsula: QMJ57778, Heathlands, 11°44'S 142°32'E, FNEQ, B. Lyon, M. Cohen; QMJ58986, 11km NE Heathlands Ranger Station, at 150m, 11°41'S, 142°39'E, FNEQ, P.J. Lethbridge, T.A. Hawkes.

This is a northern extension of the range of this species by 600km. Both Heathlands specimens were found in low heath with sclerophyll emergents on sand.

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COURTS AND SEASONAL ACTIVITIES AT THEM BY MALE TOOTH-BILLED
BOWERBIRDS, *SCENOPOEETES DENTIROSTRIS* (PTILONORHYNCHIDAE)

CLIFFORD B. FRITH AND DAWN W. FRITH

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Court seasonality and maintenance of male Tooth-billed Bowerbirds *Scenopoeetes dentirostris* were studied over the display seasons of 1978, 79 and 80 in a 50ha upland rainforest study area on the Paluma Range, north Queensland. Seasonality of court establishment was also recorded during nine subsequent seasons. Initial court establishment varied from season to season, the abundance of fruit in the study area having a greater influence than temperature and/or rainfall. Lack of rain and associated higher temperatures and fruit crop size influenced court decoration and maintenance levels at established courts during the display season. The onset of the wet season usually terminated court activity but significant dry spells thereafter caused a brief return to courts and their maintenance. Excessively dry, seasonally abnormal conditions caused a cessation of court activity altogether. The size of the cleared court area of more established courts of older males varied greatly, the largest being 2.75 X 1.95m and the smallest 1.0 X 0.8m. Partly established, temporary, courts of presumed younger males were smaller. Mean number of leaves on courts during peak display activity was 69. Of newly placed fresh leaves 79% were removed from courts within a week. During peak display activity a mean of 6.3 leaves were placed on courts/day and a mean of 6.9 removed. The turnover of leaves as court decorations was highest during hot dry spells. Leaves of *Polyscias australiana* were conspicuously favoured as court decoration by older males and the vast majority of leaves stolen from courts were of this plant. That leaves of a given tree species favoured by males as court decorations varied between age classes of males and geographical areas suggests the influence of local tradition based on imitative learning, as has been recorded in males of other polygynous bower-building bowerbirds. Results of leaf-marking experiments lend some support to the hypothesis that a male social hierarchy is established and maintained within groups of more densely dispersed and possibly older males, by leaf stealing. Leaf stealing was most frequent between immediate neighbours, more so between those with smallest nearest neighbour distance.

Attendance levels and behaviours of male Tooth-billed Bowerbirds at their courts were monitored throughout display seasons 1979, 80 and 89. Males spent an average 64% (range 52-79%) of daylight period (0600-1800) at their courts during peak display activity. Duration of a court visit averaged 23mins, most of which (96%) was spent singing from favoured court perches, the remaining time being spent decorating/maintaining the court (1.2% of total time) or displaying (<1% of total time). Males adopted a static posture when an unidentified intra- or inter-specific bird visited their court. Males performed loud and prolonged advertisement song followed by quiet and brief display vocalisations at courts. Advertisement song included a large proportion of avian mimicry the repertoire of which was added to opportunistically. Loud and complex vocalisations appear to substitute for epigamic plumage and a sophisticated bower in this cryptically-plumaged sexually monomorphic, simplistic court-clearing polygynous bowerbird. This represents an atypical set of evolutionary adaptations to polygyny in the bowerbirds that is, however, paralleled in several similarly atypical members of the evolutionary convergent but non-bower-building polygynous Cotingas (Passeriformes, Cotingidae) of the neotropics. □ Court seasonality, leaf decoration, leaf turnover rates, leaf theft, male attendance, court behaviour, court vocalisations, Queensland, Australia, Tooth-billed Bowerbird, *Scenopoeetes dentirostris*.

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The Tooth-billed Bowerbird *Scenopoeetes dentirostris* lives in upland rainforests at 600-1400m above mean sea level, from Mt Amos (15°42'S, 145°18'E) southward to Mt Elliot (19°30'S, 146°57'E) just south of Townsville (Frith & Frith, 1985a; Nix & Switzer, 1991). The Tooth-bill is an atypical bowerbird in that although males are promiscuous and females

uniparental, it is cryptically plumaged, sexually monomorphic (Gilliard 1969, Donaghey et al., 1985; Frith & Frith, 1985a, 1989, 1990a,b, 1993, 1994) and males form exploded leks (Frith, 1993).

Unlike males of other polygynous bowerbird species, male Tooth-bills do not construct stick bowers but instead clear leaf litter from an area on the forest floor (Borgia, 1986). This 'court' encompasses the trunk of at least one 'display tree'. The males place leaves, with their paler sides uppermost, onto the cleared area and perform courtship displays upon it (Frith & Frith, 1993). The court location is advertised by loud male vocalisations that deter rivals and attract potential mates, and the arrival of a female Tooth-bill stimulates the male to drop onto his court and display (Marshall, 1954; Warham, 1962; Frith & Frith, 1993). It is assumed that females assess male quality on the basis of vocalisations, displays, courts, decorations and perhaps male attendance (time investment) before soliciting and mating. Outside the display season Tooth-bills are mostly silent and secretive inhabitants of the forest canopy.

That male bowerbirds steal decorations from the bowers of rival males, with a preference for particular colours and items, has long been known (Marshall 1951, 1954 & references therein), but has been only briefly alluded to with the Tooth-bill (Frith & Frith, 1993). In recent years bower decoration theft has been studied intensively and it has been demonstrated that males steal predominantly from immediate neighbours (Borgia, 1985a), preferentially steal items rare in the birds' environment (Borgia & Gore, 1986; Frith & Frith, 1990c) and that the greater numbers of more favoured or stolen decorations on a bower positively influenced relative male mating success (Borgia, 1985a,b; Pruett-Jones & Pruett-Jones, 1993).

Frith & Frith (in press) found that 71% of individually-marked ($n = 24$) male Tooth-bills attended only one court site, that mean annual survival rate averaged 88% and mean expectancy of further life after banding was 8.1 years. Courts of Tooth-bills have been known to persist at one site for 16 years (Frith & Frith, in press), those of the Satin Bowerbird *Ptilonorhynchus violaceus* for up to 30 years (Vellenga, 1980), and those of the Great Bowerbird *Chlamydera nuchalis* and Golden-Bowerbird *Prionodura newtoniana* for more than 20 years (Frith & Frith, unpubl. data).

Temporal and spatial animal distributions are considered indicative of environmental pressures

and the presence/absence of conspecifics (Brown & Orians, 1970). Whilst studies of bowers and/or bird activities at bowers are numerous, no study has fully documented male bower maintenance seasonality over one or more seasons and attempted to relate the so defined 'bower' or 'display' season to environmental factors such as climate and food resources. Marshall (1951) noted that the Tooth-bill display season varied from year to year. Vellenga (1970) observed that male Satin Bowerbirds in New South Wales had a display season of early August to late October, and that year to year variations possibly related to the irregular flowering of banksias and eucalypts and summer bushfires 'which affected food supplies'. No studies have attempted to relate such seasonality to the temporal availability of females which, in the case of the sexually monomorphic and secretive Tooth-bill, would be extremely difficult.

The display season of the male Tooth-bill starts with calling and court clearance. On the Paluma Range the season started in September or early October (Frith & Frith, 1993). The display season continues through to January or early February. Adult males perch above or adjacent to their court where they are conspicuously vocal, incorporating fine mimicry of other bird calls, and other sounds, into their repertoire (Frith & Frith, in press). All bowerbirds regularly attending and vocalizing at bowers have proved to be male (Marshall, 1954; Vellenga, 1980; Gilliard, 1969; Cooper & Forshaw, 1977; Frith & Frith, 1993). As there is no evidence that female bowerbirds attend and vocalize at bowers for any length of time we assume that all Tooth-bills doing so were male. The results of our long-term observations of Tooth-bills support this assumption (Frith & Frith, in press).

Male Tooth-bills spend most time at their courts performing loud and prolonged court-advertisement vocalisations, including avian mimicry, from several favoured perches immediately above or adjacent to the court (Marshall, 1954; Cooper & Forshaw, 1977; Warham, 1962). Remaining time at courts is spent maintaining and/or decorating the court or displaying. Most displays are performed on the court, are started at the base of a display tree, and are accompanied by a complex 'subsong' of avian mimicry (Frith & Frith, 1993). As interspecific mimicking by Tooth-bills has long been noted or denied in the literature (Frith & Frith, 1993) we provide both qualitative and quantitative data of it.

Males of other polygynous passerines that attend and maintain a traditional courting perch(es) or area, to which they attract females by vocalisations, have been found to be predominantly frugivorous or nectarivorous and, as a consequence, have been able to devote a high proportion of daylight hours to attending and advertising their traditional location (Snow, 1962, 1976, 1982; Snow & Snow, 1988). For some predominantly insectivorous polygynous passerines, however, see Beehler (1989).

In this paper we describe the characteristics of Tooth-bill courts with reference to leaf decorations, leaf turnover rates and inter-court leaf theft rates and patterns. Court seasonality and maintenance over three display seasons (1978-80) are discussed in relation to fruit crop, rainfall and temperature. Seasonality of court establishment was also recorded during nine subsequent seasons. Male attendance levels, behaviours and vocalisations were monitored over three display seasons (1979, 80 and 89).

METHODS

STUDY AREA, CLIMATE AND PHENOLOGY

The study was performed in 50ha of upland tropical rainforest, altitude c. 875m, on the Paluma Range (19°00'S, 146°10'E), NE Queensland, 7km from Paluma Township and 80km north of Townsville. The rainforest, classified as simple notophyll vine forest by Tracey (1982), occurs at c.600-1000m altitude. Because the Queensland Forestry Department selectively logged the study area c.1938, the canopy was uneven and disturbed, varying from c.17.5-25m high, with taller emergents. The understorey was dominated by lawyer palms, *Calamus* spp., terrestrial ferns including *Cyathea* spp., and saplings. Medium-sized woody lianes and climbing pandans, *Freycinetia* spp., were common.

The 1 × 0.5km forested study area (Fig. 1) was permanently gridded using compass, measuring tape and metal stakes, 25ha into 25 × 25m squares and the remainder into 25 × 50m rectangles. Topography to the north of the road was a flattish ridge c.30-50m wide and 600m long with a discrete knoll (= Tooth-bill Hill). Other terrain to the north was steep and dissected by gullies. Of the area to the south of the road, that to the NE was flat with less dense forest interspersed with disturbed patches of *Calamus*-dominated undergrowth. The central southern area sloped gently from the road into a system of creeks, with a few low ridges. The west end was

another rise, less discrete than Tooth-bill Hill, contiguous with a flattish c.75m wide ridge sloping down toward the southern corner of the area.

Annual rainfall and temperature show marked seasonality. The dry season extends from April-November with June-August being the driest and coldest months. The hotter wet season is from December-March. Rainfall figures were provided by the Paluma meteorological substation for the years 1978-1990. Mean annual rainfall was 2379mm during the study period. Maximum-minimum temperatures were recorded in a standard screen located 20m from the edge of the rainforest from 1 August 1978-February 1981. To obtain fruiting phenology data we examined 602 trees from September 1978-April 1979, and thereafter c.500 of these trees at six-weekly (July 1979-August 1980) or eight-weekly (November 1980-February 1981) intervals. Only trees with a girth at breast height of >32cm were examined in two sample plots, each measuring 500 × 5m, along ridges inhabited by court-owning Tooth-bills.

DEFINITIONS

We refer to a display season by the year in which it started. By 'court' we mean a cleared terrestrial area and 'site' describes the location of a court or its immediately adjacent replacement court(s). A 'traditional' court site was one attended in the same location for at least two years. A 'traditional court owner' was an individually marked court-attending bird known to attend that court in a previous season(s). A 'court tree' is any tree or sapling rooted within the cleared court area and a 'display tree' is an individual tree or sapling trunk rooted within a court area that is used by a male in initial display activity (Frith & Frith, 1993). Attendance refers to known, individually marked, males perching, calling, displaying or maintaining their own court. Thus a male visiting the court of another to steal a leaf was not attending it. As we could see only the male during most displays we refer to them only as 'displays' as distinct from 'courtship displays'.

COURT SEASONALITY AND MAINTENANCE

Intensive fieldwork was performed from 1 August 1978-28 February 1981, apart from 1 May-18 July 1979 when we were absent. This included the three display seasons 1978, 79 and 80 and non-display months March-April 1979 and March-August 1980. We divided the display seasons 78, 79 and 80 into three periods based on the degree and kind of activity at courts. 'Pre-

attendance levels at courts were monitored during 7-28 November of peak activity and 8 December of post-peak activity during season 1979, and between 1 October-28 December of peak activity and 29 January-14 February of post-peak activity during season 80. The same eight court sites were monitored during both seasons, six of the eight males attending the same court throughout. The other two males were unmarked during 79 but were possibly the same birds we individually marked at their courts in 80. During seasons 79 and 80 male attendance was monitored simultaneously at two courts, at one by direct observation by DWF from a hide while tape-recording sound, and at another by tape recording sound only. The microphone was placed at the perimeter of the court and camouflaged with leaf litter. DWF started each three hour direct observation ten minutes after being put in the hide by CBF, but earlier if the male returned to his court and behaved normally. When a twelve hour cycle (i.e. 0600-1800h) was completed at a pair of courts we repeated it, but then making the direct observation at the court previously only tape recorded. Thus both calling and silent behaviours of all males were observed, as a control in order to enable us to interpret audio-recordings made in our absence. A total of 96 and 220h of sound were audio-recorded at eight courts during peak activity of seasons 79 and 80 respectively, of which 48 and 110h respectively were accompanied by direct observations. A total of 6 and 18h of audio-recordings were made during post-peak activity of seasons 79 (during 1200-1500h) and 80 (0900-1200h) respectively.

During peak activity (17 October-22 December) of season 89 four males were monitored at their courts by direct observation by DWF during three hour watches for a total of 119 hours. One site (35) was attended by the same individual that had attended it during 79 and 80, a different male attended site 33, and the other two sites were not previously examined. Each male was radio-tagged with a 4 Biotrack single stage radio-transmitter (SS-1), using a tail mount, and was radio-tracked by G. Moore using a Telonics (U.S.A.) Tr-2 receiver with a Yagi antenna (Custom Electronics, U.S.A.). This enabled us to determine whether a silent male, unseen by the observer in the hide, was in fact present above his court.

Male activities at courts were classed into advertisement song, court maintenance, display, and silence, each being monitored. The number of court perches used for advertisement song by

the same four marked males (at sites 18, 28, 33 & 35; Table 3) during 79 and 80 were noted and time spent on each recorded during direct observation. Male vocalisations, including mimicry, performed at courts during 79 and 80 were analysed to determine whether they differed between individuals, seasons or years.

RESULTS

COURT SEASONALITY AND MAINTENANCE

The display season was started by males calling above uncleared or slightly cleared and decorated court sites. Initially only 1-5 leaves were placed on a site with little or no ground clearance. Placement of leaves and ground clearance subsequently increased simultaneously through pre-peak activity. Courts were well established by the third to fourth weeks of September during seasons 80, 83, 85, 87 and 88, and by the third to fourth week of October during seasons 78, 79, 81, 82, 84 and 89.

Detailed results from display seasons 79, 80 and 81 are summarised in Figure 2. Differences between those seasons may be related to differences in climate and phenology (Fig. 3) and these are discussed below.

Season 78. Males started calling on 27 September and pre-peak activity started between 29 September-5 October and lasted three weeks (Fig. 2). This period was dry (9mm of rain over five days of rain) and mean weekly temperatures were 20.9-21.8°C. Peak activity started 20-26 October with all courts well cleared and decorated with many leaves (mean = 73.1, SD = 34.7) and faecal samples accumulating. This phase lasted ten weeks, until 28 December, during which 441mm of rain fell over 43 rain days and mean weekly temperatures were 18.0-27.8°C (mean of means = 22.9°C). Post-peak activity lasted seven weeks. Courts deteriorated during heavy early January rains but some faeces indicated males were still attending, but were not maintaining, courts. During 19-25 January, the rain eased and courts were re-cleared, decorated and attended but this activity was brief and declined after a few subsequent days of increased rain. By 15 February all courts were derelict (Fig. 2).

Season 79. On 12 September some males were calling above 10 known but uncleared traditional sites. Court establishment began during 15-21 September and pre-peak activity lasted five weeks (Fig. 2). This period was dry (37mm of rain over nine rain days) and mean weekly temperatures were 19.1-20.9°C for three weeks, rising to

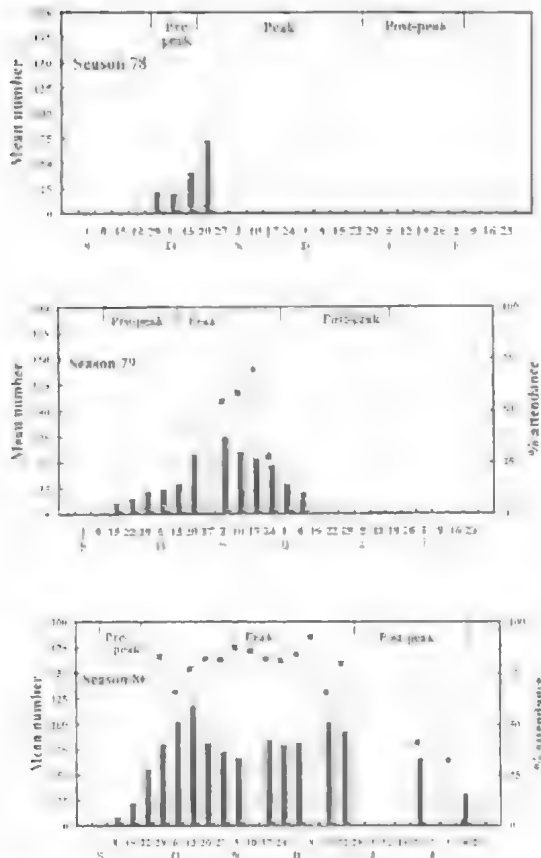


FIG. 2. Court maintenance and attendance by male Tooth-billed Bowerbirds at courts during pre-peak, peak and post-peak activity of display seasons 78, 79 and 80. Note: Solid column = mean number of court leaves (pre-peak $n = 5-25$ courts, peak & post-peak $n = 5$ courts); Clear column = mean number of defaecated seeds (pre-peak $n = 5-10$ courts, peak & post-peak $n = 10$ courts); Line = % of time males attended courts ($n = 8$ males).

24.5°C. Peak activity started 20-26 October and lasted six weeks, until the end of November, whilst remaining extremely dry and hot (51mm of rain over 13 rain days) with mean weekly temperatures of 21.5-24.8°C (mean of means = 23.9°C). Leaf numbers peaked (mean = 75, SD = 31.0) between 3-9 November but had declined by the end of November. Male attendance levels remained high until 23 November. This suggests that while males were attending courts they were not maintaining them during these extremely dry conditions. There were significantly fewer leaves on courts when less rainfall preceded counts ($r_s = 0.97$, $P < 0.05$) and mean weekly temperatures were higher ($r_s = 0.92$, $P < 0.05$). Post-peak ac-

tivity lasted eight weeks. During 1-21 December it remained extremely dry (0.2mm of rain) and hot with mean weekly temperatures of 24.6-28.3°C (mean of means = 26.2°C). Activity at courts rapidly declined and ceased by 21 December. Rain started on 25 December and on 8 January, when rain eased, there was a brief period of renewed court activity for two weeks, but courts subsequently became derelict with no further activity or calling during the extremely wet late January and February (Figs 2, 3B).

Season 80. Pre-peak activity was early, starting on 27 August when a Tooth-bill was calling above an uncleared traditional site. No traditional sites ($n = 10$) were cleared on 1 September but between 8-14 September a few were partly established and within two weeks, during which no rain fell and mean weekly temperatures were 21.3-24.4°C, courts were well established (Fig. 2). Peak activity started 22-28 September and lasted 14 weeks, to 28 December, during which 298 mm of rain fell over 20 rain days and mean weekly temperatures were 21.2-25.2°C (mean of means = 23.0°C). Leaf numbers reached a maximum (mean = 119.4, SD = 50.1; Fig. 2) between 13-19 October. During the next three weeks the numbers of leaves on courts declined, although court attendance levels remained high. Leaf numbers increased again during mid-December. There were more leaves on courts when male attendance levels were relatively lower and this correlation was significant ($r_s = 0.32$, $P < 0.1$). There were significantly fewer leaves when less rainfall preceded counts ($r_s = 0.72$, $P < 0.01$) and when temperatures were higher ($r_s = 0.54$, $P < 0.05$). Courts were still maintained and attended at the end of December, but all activity stopped when torrential January rains started (Fig. 3B). Post-peak activity lasted nine weeks. Courts became waterlogged, leaves rotted in situ, and no attendance or maintenance took place. Between 26 January-1 February courts were re-cleared and decorated as rain eased (Figs 2, 3B). During February, when it again rained heavily (Fig. 3B), courts deteriorated, few leaves were added, and whilst some faeces were collected, court attendance levels were low. This indicated that males were seldom maintaining, or perching at, their courts.

Non-display seasons. We heard Tooth-bills calling above traditional court sites during March and/or April of seasons 78, 79, 80, 81 and 83, after wet season rains eased. During March 1980 we found 15 traditional court sites to be uncleared, or slightly cleared, but decorated (<12 leaves).

Males then called above court sites with much mimicry. We identified one male as the marked traditional site owner but two birds, at sites usually occupied by traditional marked males, were unbanded 'intruders'. On 11 June, we heard a bird calling above an uncleared, undecorated, traditional court site. Between 19-23 June we examined ten traditional sites to find six uncleared or slightly cleared and decorated (< nine leaves) and males calling infrequently above them. All courts were derelict by 3 July. During five other winter seasons no similar activity was observed. The observed winter activity may have related to an abundant fruit crop at that time (Fig. 3C).

COURT CHARACTERISTICS AND DECORATIONS

Size and form. Of 59 courts attended in peak activity of season 89, 54 were well established and five partly so (see below). Of the 54 well established courts, three were almost circular and 51 were oval. The largest oval court measured $2.75 \times 1.95\text{m}$ (we have seen one $3.65 \times 2.1\text{m}$ elsewhere) and the smallest $1.0 \times 0.8\text{m}$. Mean length of the longer oval court axis was 1.96m ($SD = 0.35$, $n = 51$), and of the shorter 1.31m ($SD = 0.34$, $n = 51$). One extremely elongate court measured $2.64 \times 0.75\text{m}$. Large courts tended to have more leaves but there was no significant correlation between court size/leaf numbers ($r_s = 0.03$, $P > 0.05$) during peak activity of season 89.

Of the 54 well established courts 50 had a tree rooted just within their cleared area. The ground to at least one side of this display tree was clean of floor litter and leaf decorations. The remaining four courts had two display trees, the ground around part of both being cleared. The display tree on most (90%) oval-shaped courts was located near one end of the longer axis. Display trees varied in size from a large sapling to a substantial tree (mean diameter at breast height = 113.6mm ($SD = 1.4$, range $30\text{--}340\text{mm}$, $n = 53$). Twenty one of the 54 courts were flat, the rest being on sloping ground. The display tree on sloping ground was usually (91%) at the higher end. Twenty of the 54 courts had lawyer canes, *Calamus* spp., growing on them. A few to 10 saplings of <30mm diameter were growing on 54% of courts. One or two heaps of germinating seeds beneath commonly-used singing perches were found on many courts.

The five partly established courts were all small. One was a $1.4 \times 0.75\text{m}$ oval and the others were circular, of <1m diameter. Two of these encompassed a, centrally located, display tree.

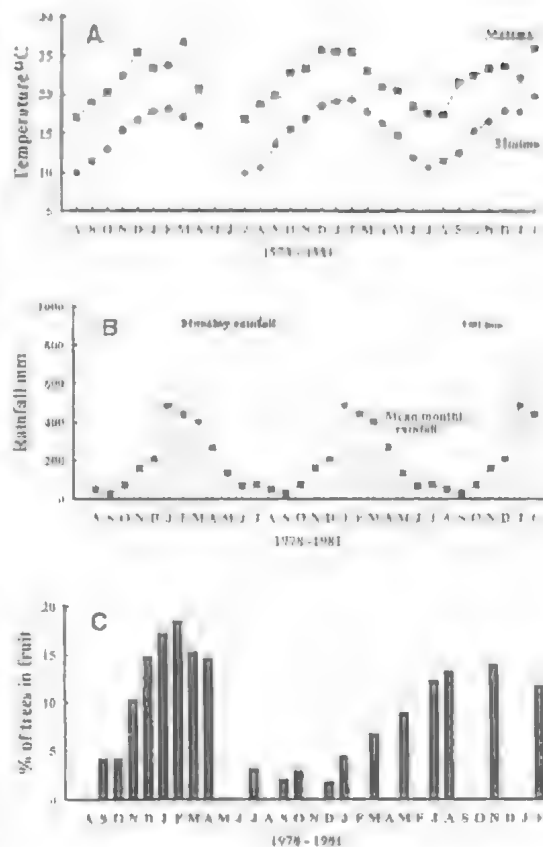


FIG. 3. Mean monthly temperature (a), mean monthly rainfall (1978-1990) (b), and monthly percentage of sampled trees in fruit (c) on the Paluma Range, north Queensland.

Leaf numbers and types. The mean number of leaves on courts during peak activity of seasons 79, 80, 81, 86 and 89 varied from 60-78 (mean of means = 69, Table 1). There were more leaves on courts during 79, 80 and 81 than during 86 and 89 but differences were not significant ($\chi^2 = 4.45$, $P > 0.30$). Variations between seasons were possibly due to the dates counts were made during peak activity (see Table 1).

The most abundant decoration leaf species (mean = 92%, Table 1) was *Polyscias australiana*, Araliaceae (= *Polyscias* in the following). Other leaves often used as decoration included *Sloanea lungii* (Elaeocarpaceae), *Cryptocarya hypospodia*, *C. mackinnoniana*, *C. putida*, *Neolitsea dealbata*, *Litsea bindoniana* (Lauraceae), *Symplocos cochinchinensis* (Symplocaceae), *Alphitonia whitei* (Rhamnaceae), *Commersonia bartramia* (Ster-

TABLE 1. Mean number of leaves and percentage of them that were *Polyscias* on male Tooth-billed Bowerbird courts during peak activity of five display seasons. (Months are indicated by their first capital letter).

| Courts and leaves | Seasons | | | | |
|---|----------------|-----------------|----------------|-----------------|----------------|
| | 79 (20O-9N) | 80 (22S-26O) | 81 (27O-9N) | 86 (15- 21D) | 89 (17-30N) |
| Number of well established courts | 21 | 36 | 17 | 46 | 53 |
| Mean number of leaves a court | 70.0 | 75.2 | 78.2 | 59.5 | 59.4 |
| Range | 20-120 | 19-179 | 44-150 | 19-108 | 20-120 |
| SD | 28.3 | 34.2 | 25.9 | 22.3 | 22.8 |
| % of total leaves that were <i>Polyscias</i> | 97 | 98 | 90 | 91 | 83 |
| Number of courts with > 90% | 20 | 34 | 12 | 34 | 21 |
| 70-90% | 1 | 2 | 4 | 7 | 20 |
| < 70% <i>Polyscias</i> | 0 | 0 | 1 | 5 | 12 |
| Number of new court sites | 3 | 6 | 1 | 5 | 7 |
| Number of partly established courts | 1 | 2 | 2 | 2 | 5 |
| Mean number of leaves a court | | 16.5 | 24.5 | 31.0 | 19.6 |
| % of total leaves that were <i>Polyscias</i> | | 84 | 73 | 63 | 52 |
| Number of new court sites | 1 | 2 | 2 | 2 | 3 |
| Court sites (n = 8) with one owner | | | | | |
| Mean number of leaves a court | 79.6 | 92.8 | 79.2 | 61.0 | 45.5 |
| % of total leaves that were <i>Polyscias</i> | 99 | 97 | 88 | 84 | 73 |
| Courts sites with 2 (n = 3) or 3 (n = 4) owners | | | | | |
| Mean number of leaves a court | 75.0 | 69.4 | 81.0 | 59.4 | 65.9 |
| % of total leaves that were <i>Polyscias</i> | 99 | 98 | 98 | 98.0 | 92.0 |

culiaceae), *Smilax australis*, *S. glycyphylla* (Smilacaceae) and *Rubus moluccanus* (Rosaceae). Leaves of *Asplenium* and *Alpinia* spp. were used seldom.

The percentage of *Polyscias* leaves on well established courts during 79 and 80 was higher than during other seasons, but these differences were not significant ($\chi^2 = 1.62$, $P > 0.80$). A lower proportion (83%) of *Polyscias* were used as decoration during 89, the remaining proportion consisting mostly (12%) of *Cryptocarya* spp.. During seasons 78 and 79, 95% of courts were decorated with >90% *Polyscias*. During seasons 81, 86 and 89, 85% of courts were decorated with >70% *Polyscias*. Seventeen courts over these five seasons had <70% *Polyscias* (range = 30-65%), and another had only 10%. Of 21 newly established sites over these five seasons, five were decorated with 70-90% and three had <70% *Polyscias* (Table 1).

The numbers of leaves on traditional courts attended by the same male during the five seasons averaged 71.6 (SD = 18.8, n = 6) and was similar (mean = 70.1, SD = 8.3, n = 7) to the numbers on traditional courts attended by two or three males over the period (Table 1). These courts were all mostly decorated with *Polyscias*.

Twelve courts were only ever partly established, during the peak activity of the five seasons. These were decorated with fewer leaves and a smaller proportion of *Polyscias* (Table 1). Ten of the 12 were at new court sites and the other two (season 89) were on traditional sites of nine and 11 seasons standing. The latter site had been attended by the same individual male during the previous 11 seasons, but during 89 was attended by an unmarked male who cleared three small separate areas < 1m apart and decorated each with a few leaves.

LEAF TURNOVER RATES

Season 79. The total number of leaves on adjacent courts (sites 6, 32, 33, 35 and 37; see Fig. 1 and 5) were counted four times over 21 days (mean sampling interval = 7 days) during peak activity and 871 newly-placed leaves were marked on them. Of these leaves, 79% were removed from courts within 7 days, 18% (1% of which had been moved from one court to another) between 7-13 days and 3% between 14-20 days. The mean number of days an initially fresh leaf remained on a court was 6.1.

There was an average of 59 leaves on each court during peak activity, courts 35 and 37 having most (Table 2). Mean numbers of leaves brought

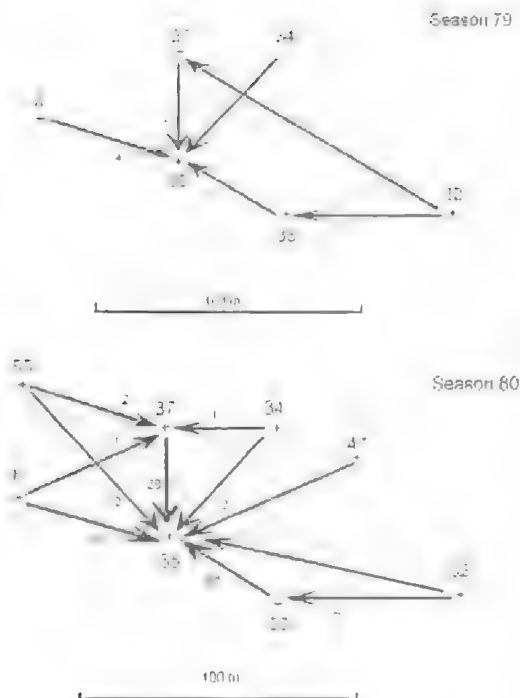


FIG. 5. Inter-court leaf theft by six (season 79) and eight (season 80) adjacent male Tooth-billed Bowerbirds on Tooth-bill Hill and slopes. Note: Large-type number by court site (+) = site number; Arrows indicate direction of leaf theft with total number of leaves involved indicated by smaller-type number beside the line.

$p = 0.008$). Similarly, more leaves were removed per day during the first half (mean = 7.4, SE = 0.67) than during the latter half (mean = 5.4, SE = 0.38) of peak activity, the difference being significant (Mann Whitney $U = 1$, $p = 0.008$). Immediately after January rains eased males removed all old leaves from courts and placed new ones on them (Fig. 4).

More *Polyscias* leaves (mean = 98%, range 93–100%) were used on these courts during the first half of peak activity than during the latter half of it (mean = 90%, range 72–93%). Fewer (mean of means = 61%) *Polyscias* leaves were used as decoration during post-peak activity.

LEAF THEFT

Season 79. Of 871 leaves marked on six adjacent courts during peak activity, ten (1%) were subsequently found on neighbouring courts. All were stolen within 7 days of being marked. Three of the six male court owners were thieves, males

at courts 33 and 37 each stealing one leaf, and the male at court 35 stealing a total of eight leaves from three neighbouring courts (Fig. 5). Daily theft rate was 0.38 leaves/day/male.

Season 80. Of 3219 leaves marked on nine adjacent courts during peak activity, 93 (3%) were subsequently found on neighbouring courts. Of stolen leaves 88% were taken within a mean of 9 days of being marked and the remainder were moved >9 days after they had been marked on the victim's court. More leaves were stolen during the first half (63% of thefts) than the latter half of peak activity. Three of the nine male court owners were thieves, these being the same individuals found to be thieves in season 79 (Fig. 5). Daily theft rate was 0.88 leaves/day/male. Most (97%) leaves stolen were *Polyscias*.

The male at court 33 stole six leaves from one neighbour, and the male at court 37 stole four leaves from three neighbours (Fig. 5). The male at court 35 was never stolen from but stole a total of 85 leaves from seven neighbouring courts (mean inter-court distance = 60.3, SD = 21.5m, range 36–95m). There was a significant correlation between number of thefts by the court 35 male and the distance he travelled to a victim's court ($r_s = 0.97$, $P < 0.01$). He stole more leaves from closer neighbours (Fig. 5) but did not steal from another neighbour, at court 38, 105m distant. Court 34, from which a single leaf was stolen, was excluded from this analysis as it was not established until the last two weeks of peak activity. Neighbouring males usually stole leaves during a court owner's absence. On four occasions, however, we watched the bird from site 35 remove a leaf from site 33 whilst the owner continued singing above it.

MALE ATTENDANCE LEVELS AT COURTS

Seasonal variation. During peak activity of seasons 79, 80 and 89 males spent an average of 52, 79 and 61% respectively of time attending courts. The proportion of total time individual males spent at courts during peak activity (Table 3) varied significantly during season 79 ($\chi^2 = 26.5$, $P < 0.001$) but not during 80 ($\chi^2 = 2.25$, $P > 0.90$) or 89 ($\chi^2 = 2.81$, $P > 0.30$). Males spent an average of 25 (range 18–31, SE = 1.58), 22 (range 17–27, SE = 1.18) and 21 (range 20–25, SE = 1.03) mins at the court per presence during seasons 79, 80 and 89 respectively (Table 3). Thus, despite lower attendance levels during season 79 and, to lesser extent, during 89, once males were at their courts the duration of each visit was similar. Mean duration per absence from

TABLE 3. Court attendance levels by individual male Tooth-billed Bowerbirds during peak activity of display seasons 79, 80 and 89.

| Season | Site number | HOURS | | ABSENCE | | PRESENCE | |
|------------------|-------------|------------------|--------------|---------------------|------------------------|----------------------|-------------------------|
| | | Audio-recordings | Observations | Mean mins @ absence | % of total time absent | Mean mins @ presence | % of total time present |
| 79 | 18 * | 12 | 12 | 23.5 | 55.5 | 18.9 | 44.5 |
| | 28 * | 12 | 12 | 15.0 | 35.4 | 25.8 | 64.6 |
| | 33 * | 12 | 12 | 32.4 | 67.6 | 18.0 | 32.4 |
| | 35 * | 12 | 12 | 23.5 | 45.8 | 28.0 | 54.4 |
| | 6 * | 12 | | 37.4 | 62.4 | 24.6 | 37.6 |
| | 17 | 12 | | 16.0 | 37.7 | 28.0 | 62.3 |
| | 21 | 12 | | 13.0 | 27.2 | 30.9 | 72.8 |
| | 32 * | 12 | | 24.0 | 53.1 | 24.1 | 47.0 |
| Total / Mean / % | | 96 | 48 | 22.5 | 48.0 | 24.9 | 52.0 |
| 80 | 18 * | 27 | 12 | 8.2 | 22.6 | 25.6 | 77.4 |
| | 28 * | 26 | 17 | 5.1 | 16.0 | 23.8 | 84.0 |
| | 33 * | 30 | 18 | 7.6 | 25.7 | 20.6 | 74.3 |
| | 35 * | 27 | 21 | 5.3 | 21.1 | 20.0 | 78.9 |
| | 6 * | 27 | 6 | 7.9 | 29.6 | 17.0 | 70.4 |
| | 17 | 27 | 15 | 4.9 | 17.9 | 21.8 | 82.1 |
| | 21 | 26 | 9 | 5.3 | 15.1 | 27.1 | 84.9 |
| | 32 * | 30 | 12 | 4.7 | 17.1 | 19.9 | 82.9 |
| Total / Mean / % | | 220 | 110 | 6.1 | 20.7 | 21.6 | 79.3 |
| 89 | 33 | 23 | 23 | 16.9 | 44.1 | 20.3 | 54.3 (1.8) ** |
| | 35 * | 24 | 24 | 17.7 | 39.2 | 24.7 | 58.4 (2.4) |
| | 23 | 36 | 36 | 13.6 | 37.9 | 20.4 | 59.4 (2.7) |
| | 37 | 36 | 36 | 8.4 | 27.0 | 21.6 | 71.9 (1.1) |
| Total / Mean / % | | 119 | 119 | 13.1 | 38.0 | 21.6 | 62.0 (2.0) |

* = same male owner each season

** in parenthesis = % total time males were present but detected only by radio-tracking.

courts during season 80 was much briefer and far less variable between individual males (range 5-8mins, SE = 0.53) than during 79 (range 13-37mins, SE = 3.02) or 89 (range 8-18mins, SE = 2.11).

During season 89 transmitters on the four radio-tagged males enabled us to learn that they spent 1.1-2.7% (mean = 2) of time silently in the forest canopy above their court, this figure being similar during different months of peak activity, and times of day. Thus, figures for absence of other males, lacking radio-tags, during seasons 79-80 (Tables 3-5) could include an error of up to 3% and figures for time present could be higher by up to 3%. This potential error was not taken into account in time-budgeted court activity data presented for season 89 (Tables 6-8).

Monthly variation. Peak activity lasted six weeks (20 October-30 November) during season 79, 14 weeks (22 September-28 December)

during 80 (Fig. 2), and 11 weeks (13 October-28 December) during 89. Season 79 was excessively dry and, although December rainfall was near average, it did not start raining until 25 Decem-

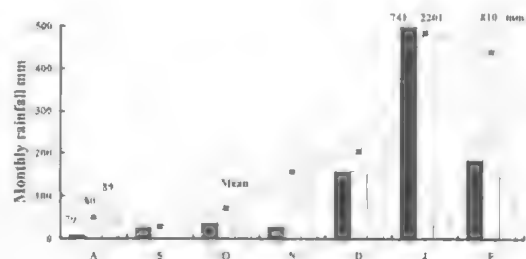


FIG. 6. Monthly rainfall during display seasons 79, 80 and 89 and mean monthly (= ■) for 1978-1990 on the Paluma Range, north Queensland.

TABLE 4. Monthly court attendance levels by male Tooth-billed Bowerbirds during peak (seasons 79, 80 & 89) and post-peak (79 and 80) activity.*

| Season | Months | Hours of audio-recordings | ABSENCE | | PRESENCE | |
|-----------|----------|---------------------------|---------------------|------------------------|----------------------|-------------------------|
| | | | Mean mins @ absence | % of total time absent | Mean mins @ presence | % of total time present |
| 79 | | | | | | |
| Peak | November | 96 | 22.5 | 48.0 | 24.9 | 52.0 |
| Post-peak | December | 6 | | 100.0 | | |
| 80 | | | | | | |
| Peak | October | 78 | 6.4 | 23.0 | 18.3 | 77.0 |
| | November | 81 | 4.9 | 16.8 | 22.2 | 83.4 |
| | December | 61 | 7.5 | 23.2 | 24.5 | 76.8 |
| Post-peak | February | 18 | 27.4 | 66.0 | 15.3 | 34.0 |
| 89 | | | | | | |
| Peak | October | 47 | 13.4 | 34.1 | 23.6 | 63.6 (2.3) ** |
| | November | 36 | 9.7 | 28.6 | 22.8 | 69.7 (1.7) |
| | December | 36 | 16.3 | 46.0 | 17.6 | 52.0 (1.9) |

* = court sites and sample sizes as in Table 3

** In parenthesis = % total time males were present but detected only by radio-tracking

ber. Little or no rain fell during September 80 or 89, and October rainfall of those seasons was below average, November 79 was dry, and November 89 wet (Fig. 6).

Court attendance levels were higher during each month of season 80 than during each corresponding month of 79 and 89. Attendance levels reached a peak in November of seasons 80 and 89. Court attendance levels were lowest during November 79 and December 89. Mean duration per presence at courts varied little between the respective months of each season. Mean duration per absence from courts was notably low during all months of the 80 season. During the extremely dry early December 79 court attendance stopped. During season 80 there was a brief return to post-peak activity when torrential January rains stopped but attendance levels were low, males spending little time at courts each visit (Table 4).

Daytime variation. Court attendance levels were always highest during the period 0600-0900h. During season 79 attendance declined during the latter

of day (Tables 6-8).

Mean duration of advertisement song periods was similar during seasons 79 (range 19-30mins, SE = 1.46), 80 (range 17-27mins, SE = 1.18) and 89 (range 20-27mins, SE = 1.31, Table 6). Mean duration of song periods was similar each month of peak activity except during December 89 when seasonal activity declined. It was also much lower during post-peak activity of season 80 (Table 7).

TABLE 5. Variation in daytime court attendance levels by male Tooth-billed Bowerbirds during peak activity of display seasons 79, 80 and 89.*

| Season | Time | Hours | ABSENCE | | PRESENCE | |
|--------|-----------|-------|---------------------|------------------------|----------------------|-------------------------|
| | | | Mean mins @ absence | % of total time absent | Mean mins @ presence | % of total time present |
| 79 | 0600-0900 | 24 | 14.6 | 35.5 | 25.8 | 64.5 |
| | 0900-1200 | 24 | 20.0 | 48.6 | 20.6 | 51.4 |
| | 1200-1500 | 24 | 21.8 | 45.5 | 27.1 | 54.5 |
| | 1500-1800 | 24 | 39.2 | 62.6 | 28.4 | 37.4 |
| 80 | 0600-0900 | 48 | 4.4 | 16.2 | 20.6 | 83.8 |
| | 0900-1200 | 60 | 7.0 | 23.2 | 21.6 | 76.8 |
| | 1200-1500 | 60 | 6.7 | 22.7 | 20.6 | 77.3 |
| | 1500-1800 | 52 | 6.1 | 19.7 | 23.9 | 80.3 |
| 89 | 0600-0900 | 29 | 8.2 | 27.4 | 19.5 | 70.7 (1.9) ** |
| | 0900-1200 | 30 | 16.1 | 40.1 | 21.8 | 58.1 (1.8) |
| | 1200-1500 | 30 | 15.1 | 41.9 | 20.0 | 55.5 (2.6) |
| | 1500-1800 | 30 | 14.1 | 34.5 | 25.6 | 63.9 (1.6) |

* = court sites and sample sizes as in Table 3

** In parenthesis = % total time males were present but detected only by radio-tracking.

part of the day (Table 5). During season 80 court attendance levels remained high throughout the day. Mean duration per presence at courts did not vary greatly at differing times of the day over each season (Table 5).

MALE BEHAVIOUR AT COURTS

Advertisement song. Male Tooth-bills spent most (mean of means = 95.7%) of their time at courts giving loud advertisement song from favoured perches. This was similar for all males (range 90-98%) during each season, each month of peak activity and different times

TABLE 6. Time-budgeted activities performed by individual male Tooth-billed Bowerbirds at courts during peak activity of display seasons 79, 80 and 89. *

| Season | Court site number | ADVERTISEMENT SONG | | MAINTENANCE | | DISPLAY | | SILENCE ** | | TOTAL TIME PRESENT (mins) |
|------------------|-------------------|-------------------------|---------------------------|--------------------------------|-------------------------------|----------------------------|------------------------------|----------------------------|--------------------------------|---------------------------|
| | | Mean mins @ song period | % of time present singing | Mean mins @ maintenance period | % of time present maintaining | Mean mins @ display period | % of time present displaying | Mean mins @ silence period | % of time present spent silent | |
| 79 | 18 * | 19.4 | 96.9 | 1.3 | 1.9 | 1.4 | 0.9 | 1.0 | 0.3 | 321 |
| | 28 * | 25.3 | 98.4 | 0.8 | 0.8 | 1.9 | 0.4 | 1.0 | 0.4 | 465 |
| | 31 * | 19.0 | 89.6 | 2.0 | 1.7 | 1.8 | 3.9 | 3.7 | 4.8 | 235 |
| | 35 * | 28.5 | 94.7 | 2.3 | 1.2 | 0.0 | 0.0 | 2.0 | 4.1 | 392 |
| | 6 * | 26.1 | 96.1 | 1.0 | 0.4 | 1.1 | 1.8 | 1.3 | 1.9 | 271 |
| | 17 | 29.2 | 97.6 | 2.8 | 1.3 | 1.6 | 0.7 | 0.9 | 0.4 | 449 |
| | 21 | 30.4 | 98.4 | 1.4 | 0.5 | 1.6 | 0.9 | 0.5 | 0.2 | 525 |
| | 32 * | 23.8 | 98.4 | 1.4 | 0.8 | 0.0 | 0.0 | 0.9 | 0.8 | 336 |
| Total / Mean / % | | 25.2 | 96.7 | 1.3 | 1.0 | 1.5 | 0.8 | 1.7 | 1.4 | 2993 |
| 80 | 18 * | 25.1 | 88.2 | 1.7 | 0.7 | 1.4 | 0.3 | 0.9 | 0.8 | 1253 |
| | 28 * | 24.1 | 97.4 | 1.3 | 0.8 | 1.4 | 1.0 | 0.8 | 0.9 | 1311 |
| | 33 * | 23.7 | 94.0 | 1.5 | 2.1 | 1.7 | 1.9 | 1.3 | 2.0 | 1338 |
| | 35 * | 19.8 | 92.8 | 2.0 | 2.7 | 1.8 | 0.7 | 1.2 | 3.8 | 1278 |
| | 6 * | 18.8 | 94.1 | 1.5 | 3.0 | 1.3 | 1.2 | 0.9 | 1.7 | 1141 |
| | 17 | 23.1 | 95.8 | 1.7 | 2.4 | 1.5 | 0.4 | 1.0 | 1.6 | 1330 |
| | 21 | 26.7 | 98.7 | 0.9 | 0.4 | 1.5 | 0.2 | 0.9 | 0.7 | 1325 |
| | 32 * | 18.5 | 95.1 | 2.1 | 2.4 | 2.0 | 0.9 | 1.0 | 1.0 | 1493 |
| Total / Mean / % | | 22.0 | 95.8 | 1.8 | 1.8 | 1.6 | 0.8 | 1.1 | 1.8 | 10489 |
| 89 | 33 | 20.4 | 92.6 | 1.0 | 1.2 | 2.0 | 0.8 | 1.5 | 5.4 | 750 |
| | 35 * | 26.6 | 94.9 | 0.9 | 0.6 | 2.2 | 0.5 | 2.2 | 4.0 | 640 |
| | 23 | 22.3 | 93.9 | 1.0 | 0.8 | 1.6 | 0.2 | 1.8 | 5.1 | 1282 |
| | 37 | 23.9 | 95.4 | 1.2 | 1.1 | 1.5 | 0.4 | 1.3 | 3.1 | 1552 |
| Total / Mean / % | | 23.2 | 94.4 | 1.2 | 0.8 | 1.8 | 0.4 | 1.6 | 4.3 | 4424 |

* = same male owner each season

** = silent periods of > 30 seconds duration (see Results), but excluding maintenance time

Mean duration of song periods did not vary greatly during different times of the day over each season (Table 8).

Almost all (>99%) advertisement song was given from perches immediately above or about courts, males only rarely (<1%) singing loudly on the ground at the base of the display tree, prior to the distinctly different display subsong. Males usually sang from more than one perch during a court visit (mean = 1.9), spending an average of 13mins on each (Table 9).

Song perches were high above the court (high perches), adjacent to it (adjacent perches) or just above the court (court perches). High perches were >5m above the ground in the understorey or lower canopy, and up to 8m horizontally from the court location. Most males had two high perches (mean = 1.9). Adjacent court perches were mostly horizontal or sloping sapling or small tree branches, 3-5m above ground and between 1-5m from the court perimeter. Males used 1-4 adjacent perches (mean = 1.8). Court perches were horizontal branches of saplings and, less commonly, vines or fallen branches lying across the court at 0.3-3.0m (mean = 1.4) above the cleared ground or within a metre radius of its perimeter. More court perches were used during season 80

(mean = 8.3, range 5-12) than during 79 (mean = 4.8, range 4-7).

Males spent an average of 21, 11 and 68% of total song time singing on high, adjacent and court perches respectively, spending more time singing on high and adjacent perches during season 79 than 80 (Table 9). High perch singing decreased as season 80 progressed, from 22% of October song time to 13% of November and 4% of December song time. High perches were mostly used (90% of occasions frequented) for singing when males first returned to their court area, birds subsequently flying down to their adjacent and/or court perches. Returning males sometimes flew directly to an adjacent perch and sang there before moving to a court perch or returned directly to a court perch (Table 9). Of returns to a court perch 37% were, however, via the court to place a newly-acquired leaf there.

During 0600-0900, 0900-1200, 1200-1500 and 1500-1800h males sang from high perches for 12, 19, 19 and 8% of total song time respectively. Thus, males spent more time singing on high perches during the hotter, brighter, part of the day.

Of 31 perches used by four males at court sites 18, 28, 33 and 35 during season 79, 84% were still

TABLE 7. Monthly time-budgeted activities performed by male Tooth-billed Bowerbirds at courts during peak (seasons 79, 80 and 89) and post peak (80) activity. *

| Season | Months | ADVERTISEMENT SONG | | MAINTENANCE | | DISPLAY | | SILENCE ** | | TOTAL TIME PRESENT (mins) |
|-----------|----------|-------------------------|---------------------------|--------------------------------|-------------------------------|----------------------------|------------------------------|----------------------------|--------------------------------|---------------------------|
| | | Mean mins @ song period | % of time present singing | Mean mins @ maintenance period | % of time present maintaining | Mean mins @ display period | % of time present displaying | Mean mins @ silence period | % of time present spent silent | |
| 79 | | | | | | | | | | |
| Peak | November | 25.2 | 33.7 | 1.3 | 1.6 | 1.5 | 0.3 | 1.7 | 1.4 | 2993 |
| 80 | | | | | | | | | | |
| Peak | October | 20.3 | 36.4 | 1.3 | 2.2 | 1.5 | 0.3 | 1.1 | 1.1 | 3604 |
| | November | 22.0 | 33.2 | 1.2 | 1.3 | 1.5 | 1.1 | 1.2 | 1.4 | 4054 |
| | December | 24.5 | 34.2 | 1.3 | 2.6 | 1.6 | 1.2 | 1.0 | 2.6 | 2811 |
| Post-peak | February | 13.5 | 31.8 | 0.8 | 1.5 | 1.5 | 4.5 | 3.5 | 2.6 | 367 |
| 89 | | | | | | | | | | |
| Peak | October | 25.7 | 34.4 | 1.3 | 1.5 | 1.7 | 0.5 | 1.3 | 3.6 | 1794 |
| | November | 26.7 | 35.6 | 1.0 | 0.6 | 1.7 | 0.4 | 2.0 | 3.4 | 1506 |
| | December | 17.4 | 32.9 | 1.1 | 0.5 | 2.3 | 0.1 | 1.7 | 6.5 | 1124 |

* court sites and sample sizes as in Table 3

** = silent periods of > 30 seconds duration (see Results), but excluding maintenance time

in use by the same males during 80. Of six perches used by the site 35 male during 79, all were in use during 80 and he was still using three of them during 89.

Maintenance. Male Tooth-bills spent a mean of only 1.2% of total time actually on courts and maintaining them. This figure was similar for all males each season, during different months of peak activity and different times of day (Tables 6-8). Mean length of court maintenance periods varied between males but was never >2.8mins (Table 6).

Of 104 observed court maintenance periods, 95 immediately followed a male's arrival with a leaf and nine occurred during or after singing or display and involved court clearing only. After placing a new leaf and/or performing court maintenance males hopped up to a perch to sing (72% of arrivals) or simply flew away from the court.

Number of new leaf decorations brought to the court in each three hour period was higher during season 80 (mean = 1.3) than 79 (mean = 0.8) or 89 (mean = 0.7). More leaves (60%) were brought to courts during 0600-1200hrs than during the rest of the day. Once a male had placed a new leaf on his court he usually tidied or re-arranged his fresher leaves and removed old or fallen ones to beyond the court perimeter. Males were usually silent when maintaining courts, only occasionally giving a single 'chuck' note.

Displays. Upon first noticing a conspecific near his court a male would drop to the base of his display tree to give quieter, more intense, advertisement song or, more often, would immediately

commence display 'subsong' vocalisations. On a few occasions a male adopted a static 'frozen' sleeked posture prior to subsong and display (see below). Display vocalisations and posturing are described elsewhere (Frith & Frith, 1993). Most times (83%) males performed only one display, but on a few occasions they performed a sequence of two to four immediately repeated ones.

During peak activity males spent <1% of their total time at courts displaying, the mean duration of a display (including subsong) ranging from 1.1-2.2mins (mean = 1.6, Table 6). Number of displays per three hour period was greater during the peak activity of seasons 80 (mean = 0.8) than during 79 (mean = 0.5) and 89 (mean = 0.3). The total time males spent displaying was greatest during the peak activity month of November (1.5 displays/display period) and December (0.9 displays per three hours, Table 7). Most displays were performed during 0600-0900h of seasons 79 and 80 and least during 1500-1800h (Table 8). Males continued to display during post-peak (court maintenance) activity (Table 7), in fact spending relatively more time displaying then. We could not sex birds seen to be displayed to by their appearance or behaviour. No mating was seen.

Silence. The proportion of total court attendance time males spent silently (= >30secs without calling), other than during court maintenance periods, was greater during season 89 (4.3%) than 79 (1.4%) or 80 (1.6%, Table 6). These higher 89 figures were reflected during each month of peak activity (Table 7) and different times of day (Table 8), notwithstanding up

TABLE 8. Variation in daytime-budgeted court activities by male Tooth-billed Bowerbirds during peak activity of display seasons 79, 80 and 80. *

| Season | Time | ADVERTISEMENT SONG | | MAINTENANCE | | DISPLAY | | SILENCE ** | | TOTAL TIME PRESENT (mins) |
|--------|-----------|-------------------------|---------------------------|--------------------------------|-------------------------------|----------------------------|------------------------------|----------------------------|--------------------------------|---------------------------|
| | | Mean mins @ song period | % of time present singing | Mean mins @ maintenance period | % of time present maintaining | Mean mins @ display period | % of time present displaying | Mean mins @ silence period | % of time present spent silent | |
| 79 | 0600-0900 | 25.1 | 97.4 | 1.0 | 1.1 | 1.6 | 1.1 | 1.1 | 0.5 | 528 |
| | 0900-1200 | 21.6 | 96.3 | 1.5 | 2.0 | 2.0 | 1.0 | 1.2 | 0.7 | 741 |
| | 1200-1500 | 27.9 | 95.9 | 1.0 | 0.1 | 1.5 | 1.0 | 2.1 | 3.0 | 766 |
| | 1500-1800 | 27.6 | 97.3 | 1.8 | 1.0 | 1.1 | 0.2 | 1.6 | 1.5 | 539 |
| 80 | 0600-0900 | 20.3 | 95.6 | 1.3 | 1.8 | 1.4 | 1.2 | 1.2 | 1.4 | 2414 |
| | 0900-1200 | 22.8 | 96.3 | 1.4 | 1.4 | 1.7 | 1.0 | 1.1 | 1.3 | 2765 |
| | 1200-1500 | 21.2 | 95.0 | 1.9 | 1.9 | 1.7 | 1.0 | 1.0 | 2.1 | 2765 |
| | 1500-1800 | 24.1 | 96.1 | 1.9 | 2.1 | 1.6 | 0.3 | 1.0 | 1.5 | 2506 |
| 89 | 0600-0900 | 21.7 | 95.4 | 1.0 | 1.1 | 1.4 | 0.1 | 1.1 | 3.4 | 1229 |
| | 0900-1200 | 25.4 | 94.8 | 1.2 | 0.6 | 0.0 | 0.0 | 1.6 | 4.6 | 1046 |
| | 1200-1500 | 20.6 | 94.6 | 1.5 | 1.0 | 1.8 | 0.8 | 2.0 | 3.4 | 898 |
| | 1500-1800 | 26.1 | 92.9 | 1.3 | 1.0 | 1.6 | 0.8 | 2.0 | 5.3 | 1150 |

* court sites and sample sizes as in Table 3

** = silent periods of > 30 seconds duration (see Results), but excluding maintenance time

to an additional 3% silence of potential, but undetected, presence (see Table 3). The possibility that the movements of two people radio-tracking in the area might have caused relatively longer silent periods during season 80 is considered unlikely but cannot be dismissed. There were more silent periods over 1200-1500h during 79 and 80 than at other times of day (Table 8).

Most (92%) silent periods occurred immediately before, or during, advertisement song when birds preened, changed perches, turned on their perch to face the opposite direction, or when they stopped singing to apparently listen to neighbours' calls. Having apparently noted a neighbouring male was not calling, a court owner flew immediately in the direction of the presumably unattended court to steal a leaf.

The other 8% of silent periods occurred when males adopted a sleeked 'frozen' posture. We

recorded the frozen posture 34 times (mean duration = 1.1 mins), 28 of which were performed in response to a conspecific flying toward the court. On nine of these latter occasions the male immediately followed the frozen posture with display. On the 19 other occasions he chased the conspecific, which we assume to have been a neighbouring male (sometimes confirmed by band colours). Court owners sometimes chased off potential thieves without first adopting a frozen posture, the latter usually being performed by birds apparently initially unaware of the identity or sex of the visitor. Four frozen postures occurred when we heard, but could not see, a bird land high above the Tooth-bill at its court and two were given when a Grey-headed Robin *Poecilodryas albispecularis*, flew directly to a court. This behaviour appears typical of male Tooth-bills surprised by the appearance or sound

TABLE 9. Perch type used for advertisement song by the same four male Tooth-billed Bowerbirds at courts during peak activity of display seasons 79 and 80.

| Season | HIGH PERCHES (> 5 m) | | | ADJACENT PERCHES (3-5 m) | | | COURT PERCHES (< 3 m) | | | GROUND | TOTAL SONG TIME* (mins) |
|--------|----------------------|----------------------|----------------------------|--------------------------|----------------------|----------------------------|-----------------------|----------------------|----------------------------|----------------------|-------------------------|
| | Mean mins @ perch | % of total song time | % of times used on arrival | Mean mins @ perch | % of total song time | % of times used on arrival | Mean mins @ perch | % of total song time | % of times used on arrival | % of total song time | |
| 79 | 11.2 | 26 | 90 | 21.5 | 14 | 56 | 14.7 | 59.9 | 49 | 0.1 | 1349 |
| 80 | 8.9 | 16 | 89 | 11.1 | 8 | 50 | 10.6 | 75.4 | 37 | 0.6 | 2878 |

* = direct observation watches only at court sites 18, 28, 33, & 35; see Table 3

TABLE 10. Analysis of advertisement song given by male Tooth-billed Bowerbirds at eight courts during peak activity of display seasons 79 and 80.* Court sites as in Table 3.

| Season | SQUEAL | | CHUCK | | CHUCK + BABBLE | | CHUCK + MIMICRY | | BABBLE | | BABBLE + MIMICRY | | MIMICRY | | TOTAL SONG TIME (mins) |
|--------|-------------------|----------------------|-------------------|----------------------|-------------------|----------------------|-------------------|----------------------|-------------------|----------------------|-------------------|----------------------|-------------------|----------------------|------------------------|
| | Mean mins @ phase | % of total song time | Mean mins @ phase | % of total song time | Mean mins @ phase | % of total song time | Mean mins @ phase | % of total song time | Mean mins @ phase | % of total song time | Mean mins @ phase | % of total song time | Mean mins @ phase | % of total song time | |
| 79 | 2.2 | 1.7 | 2.6 | 5.9 | 2.2 | 1.2 | 3.1 | 4.1 | 17.9 | 23.4 | 11.7 | 56.5 | 5.1 | 7.3 | 2768 |
| 80 | 1.9 | 1.7 | 1.9 | 5.4 | 2.6 | 3.3 | 2.2 | 2.9 | 7.7 | 26.7 | 6.0 | 40.1 | 4.2 | 8.9 | 2857 |

of an incoming bird as we often saw Grey-headed Robins, Chowchillas *Orthonyx spaldingii*, Eastern Whipbirds *Psophodes olivaceus*, Yellow-throated Scrub-wrens *Sericornis citreogularis*, Brush-turkeys *Alectura lathami* and Spotted Catbirds *Ailuroedus melanotis* foraging toward a court without concerning the Tooth-bill owner.

We did not witness a single aggressive encounter between Tooth-bills at a court other than an owning bird chasing off another. On a few occasions we did note two birds confronting each other in a food (fruiting) tree by facing each other with sleeked plumage and agitated vocalisations.

MALE VOCALISATIONS AT COURTS

Advertisement song content was similar in seasons 79 and 80. We could divide song into seven component calls: 'squeal', 'chuck', 'chuck + babble', 'chuck + mimicry', 'babble', 'babble + mimicry', and exclusively pure 'mimicry', changes from one to another usually being quite obvious. Calls were given in phases, a male performing a phase of 'chuck' calls, following this with a phase of 'chuck + mimicry' and so on. Each song period (= a court visit) consisted of several to many phases. Each phase lasted an average of 8 and 5 mins during seasons 78 and 80 respectively. The relative time spent giving each call component and mean length of each phase was similar each season (Table 10).

'Squeals' were squeal-like screechy notes. Phases of 'squeals' represented 1.7% of total song time and were brief (Table 10). 'Squeals' were mostly (64%) given first by returning birds or as second phase calls (19%) that usually followed 'chucks' (Table 11). Occasionally 'squeals' were again given, briefly, when a male changed perches.

'Chucks' consisted of a repeated 'chuck' note, represented 6% of total song time, and were brief (Table 10). 'Chucks' were mostly (72%) given first by returning birds (Table 11), but also followed 'squeals'. Males sometimes briefly reverted to 'chucks' after changing perches.

'Chuck + babble' and 'chuck + mimicry' were dominated by 'chuck' notes interspersed with occasional 'babble or mimicry'. These calls represented <4% of total song time and phase duration was brief (Table 10). Males sometimes gave these calls having just returned to their court instead of a 'chuck' call, but mostly they were given as second phase calls (Table 11) following 'squeals' and/or 'chucks'.

'Babble' and 'babble + mimicry', often including occasional 'chucks', were the most common calls and represented 30 and 49% of total song time respectively with long phase duration (see Table 10). Males sometimes first gave these calls upon returning to the court, but mostly they were given as second, third or fourth phase calls (Table 11) following 'chuck', 'chuck + babble' and/or 'chuck + mimicry'. Some males continuously alternated between 'babble, babble + mimicry' and/or 'mimicry'. Males gave more intense and quieter advertisement song, of 'babble' or 'babble + mimicry', immediately prior to display of a mean duration of 20.9 mins (range 0-65).

Exclusive mimicry was performed by all males, represented a mean of 8% of total song time, and each phase lasted an average of 4.7 mins (Table 10). A far larger proportion (60%) of song time involved mimicry, however, when 'mimicry', 'chuck + mimicry' and 'babble + mimicry' were combined. Mimicry usually followed 'chuck + mimicry' or 'babble + mimicry'. Cicadas, crickets, frogs, dripping water and 27 bird species were identified as models for mimicry.

We audio-recorded 1074 mins of exclusive mimicry during advertisement song over seasons 79 and 80. Of total 'mimicry' time, 43% was of Bower's Shrike-thrush *Colluricincla boweri* and 30% of medleys of various bird calls mostly dominated by that species. Mimicry of Bower's Shrike-thrush also dominated 'chuck + mimicry' and 'babble + mimicry'.

King Parrots *Alisterus scapularis* were also commonly mimicked (11% of 'mimicry'). Other bird species mimicked for a combined total of

TABLE 11. Phase sequence of each call component of advertisement song given by male Tooth-billed Bowerbirds at eight courts during peak activity of display seasons 79 and 80. * Data are expressed as % of total number of phases of each call component.**

| Call component | Phase sequence | | | | | | | | | | |
|------------------|----------------|------|------|------|------|-----|-----|------|-----|-----|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11-18 |
| Squeal | 64.0 | 19.4 | 5.6 | 5.6 | 0.9 | 1.8 | 0.9 | 0.9 | 0.9 | 0.0 | 0.0 |
| Chuck | 72.4 | 7.1 | 6.7 | 4.3 | 2.6 | 2.6 | 1.0 | 1.5 | 0.2 | 0.5 | 1.0 |
| Chuck + babble | 17.1 | 44.2 | 12.2 | 9.4 | 5.5 | 3.3 | 1.1 | 0.6 | 3.7 | 0.6 | 2.3 |
| Chuck + mimicry | 19.4 | 39.4 | 14.7 | 7.6 | 5.3 | 4.0 | 2.4 | 3.0 | 0.6 | 1.2 | 2.4 |
| Babble | 11.3 | 21.7 | 16.9 | 17.3 | 12.5 | 6.7 | 4.8 | 3.5 | 1.0 | 1.2 | 3.1 |
| Babble + mimicry | 9.3 | 18.3 | 21.6 | 17.3 | 10.7 | 7.9 | 5.8 | 2.8 | 1.9 | 1.8 | 2.8 |
| Mimicry | 7.7 | 19.8 | 27.2 | 15.4 | 10.5 | 6.5 | 4.1 | 2.8 | 2.8 | 1.2 | 2.0 |
| Display subsong | 8.3 | 3.3 | 15.0 | 23.4 | 15.0 | 8.3 | 8.3 | 10.0 | 5.0 | 0.0 | 3.4 |

* = court sites as in Table 3

** = data for seasons 79 & 80 combined. See Table 10 for total song time

13% of 'mimicry' time were: Fan-tailed Cuckoo *Cuculus flabelliformis*, Yellow-eyed Cuckoo-shrike *Coracina lineata*, Grey-headed Robin, Golden Whistler *Pachycephala pectoralis*, Chowchilla, Eastern Whipbird, Yellow-throated Scrub-wren, Little Treecreeper *Climacteris minor*, Bridled Honeyeater *Lichenostomus frenatus* and Golden Bowerbird *Prionodura newtoniana*. Bird species mimicked less frequently (combined total = 3% of 'mimicry') included: Pale-yellow Robin *Tregellasia capta*, Black-faced Monarch *Monarcha melanopsis*, Spectacled Monarch *M. trivirgatus*, Rufous Fantail *Rhipidura rufifrons*, Grey Fantail *R. fuliginosa*, Australian Fernwren *Crateroscelis gutterlairs*, Large-billed Scrub-wren *S. magnirostris*, Brown Gerygone *Gerygone mouki* and Mountain Thornbill *Acanthiza katherina*.

Tooth-bills mimicked several distinct calls of a given bird species. For example, they commonly mimicked both the whistled single note song and the 'chee-chee' greeting calls of Grey-headed Robins, both whip-crack song and the 'chip-chop' calls of Eastern Whipbirds and both squeals and rattle calls of Golden Bowerbirds. Mimicry was sometimes given opportunistically, in immediate response to calling birds, such as those of a passing flock of Crimson Rosellas *Platycercus elegans*, lorikeets *Trichoglossus* spp. or, less frequently, Sulphur-crested Cockatoos *Cacatua galerita* or Red-tailed Black-Cockatoos *Calyptorhynchus magnificus*.

Tooth-bills sometimes 'duetted' with other species including King Parrot, Grey-headed Robin, Golden Whistler, Bower's Shrike-thrush, Eastern Whipbird, Yellow-throated Scrub-wren, Little Treecreeper and Bridled Honeyeater. Neighbouring Tooth-bills also appeared to in-

stantaneously copy each others 'mimicry', 'chuck' or 'babble' calls.

Tooth-bill mimicry models changed seasonally. For example, during season 79 Fan-tailed Cuckoos were extremely vocal in the study area and their calls were mimicked by all eight males (12% of 'mimicry'). During season 80 we heard fewer Fan-tailed Cuckoos and less (1%) 'mimicry' of them. The proportion of 'mimicry' incorporated into song did not differ greatly over the three peak activity months of season 80 (October = 7%, November = 9%, December = 10% of total song time), although increasing towards peak mating time and falling to an average of 6% in post-peak activity. Moreover, it did not differ much throughout the day. During the periods 0600-0900, 0900-1200, 1200-1500, and 1500-1800h males performed 'mimicry' for 6, 10, 8 and 10% of total song time respectively over seasons 79 and 80.

Bird species that regularly called in the study area during Tooth-bill display seasons but were not, or only rarely, mimicked included the Noisy Pitta *Pitta versicolor*, Victoria's Riflebird *Ptiloris victoriae* and the Spotted Catbird. The whistled bower advertisement call of male Satin Bowerbirds and the sound of dripping water was mimicked by Tooth-bills in display subsong but not during advertisement singing.

DISCUSSION

COURT SEASONALITY AND MAINTENANCE

Male Tooth-bills started court clearing in September-October, approximately six to eight weeks before first known egg-laying (Marshall, 1951; Frith & Frith, 1985a, 1993) and increasingly attended courts from October-December (Fig.

2). Food resources are abundant at this time of year (Frith 1984; Frith & Frith, 1990, 1985b). Although Marshall (1951, 1954) suggested increasing daylight time, rising temperatures and decreasing humidity might instigate the seasonal sexual resurgence of male Tooth-bills our data do not reveal clear-cut relationships between weather patterns and variation in the initiation of pre-peak activity across years.

Pre-peak activity lasted three, five and two weeks during seasons 78, 79 and 80 respectively; interesting differences because whilst temperatures were seasonally increasing slightly, relative rainfall differed between seasons (Fig. 3a,b). Relative fruit crop, however, was poor during 79 and rich during 78 and 80 (Fig. 3c), and it is possible that this influenced these differing lengths of pre-peak activity.

Peak court activity lasted for ten, six and 14 weeks during seasons 78, 79 and 80 respectively. A prolific fruit crop became available in November 78, the 79 fruit crop failed and in season 80 peak activity was preceded and accompanied by much fruit (Fig. 3c). Late peak court activity, and nesting coincided (November-February) with the months of relatively far greater beetle abundance at Paluma (Frith & Frith, 1985a,b), Coleoptera apparently being important in the nestling diet (Jackson, 1909; Marshall, 1951). Lapses in court decoration rates during the long period of peak court attendance in season 80 (Fig. 2) coincided with increasing temperatures during drier periods. At such times court decoration leaves dry and curl quickly and extremes in these conditions, such as during season 79, may cause birds to desert courts.

The start of post-peak activity is strongly associated with persistent heavy rains of wet season months January-February but during season 79 it preceded this due to excessively dry conditions (Fig. 3b). Significant dry spells within the wet season rains stimulated a brief return to renewed court activity. Warham (1962) correctly thought the onset of the wet season caused cessation of court attendance and the start of moult.

During March-April of several seasons we observed some males calling and poorly clearing and decorating courts. This would appear to be a post-moult activity performed mostly by sub-adult males, as occurs in other bowerbird species (Frith & Frith, unpubl. data). Similar behaviour was also observed in June-July 1980, which may have related to an abundant winter fruit crop (Fig. 3c) that supported a subsequent early start to the 80 display season.

COURT CHARACTERISTICS AND DECORATION

Marshall (1954) found the average number of leaves on a Tooth-bill court to be c.40 and the maximum 103 whereas Schodde & Tidemann (1988) give an erroneously low 8-15 leaves/court. Grant & Laurance (1991) found an average of 23-95 leaves a court for their 27 September-17 December study and an average of 52 leaves to 15 October and only 37 thereafter. We recorded an average of between 60-78 per season and a largest number of 108-179 leaves per court over five seasons (Table 1). Chaffer (1984) gained the impression that fewer leaves were used if they were of larger size but this could not be tested in our study area where birds preferred plant species with smaller leaves.

Male Tooth-bills in this study decorated courts predominantly with *Polyscias* leaves (Table 1) and only infrequently with leaves of 14 other tree species. Jackson (1910) listed the 14 most commonly used leaves he found on Atherton Tableland courts but does not include *Polyscias*. Marshall (1954) lists identifications of 181 leaves from five Atherton Tableland courts and does not include *Polyscias* which are, however, used by Atherton Tableland birds (Frith & Frith, unpubl. data). Grant & Laurance (1991) found that decorations on 13 Atherton Tableland courts consisted of >90% *Schefflera actinophylla* leaves. These facts suggest geographic variation in favoured court decorations, a situation found in bower decorations of the two Satin Bowerbird subspecies (Chaffer, 1984; Frith & Frith, unpubl. data) and between populations of the Vogelkop Bowerbird *Amblyornis inornatus*. Diamond (1986, 1987) considered this to be indicative of local tradition based on imitative learning.

Whilst traditional court-owning Tooth-bills at Paluma very predominantly used *Polyscias* leaves we noted that courts established at new sites or traditional sites that were only partly re-established during a season had fewer *Polyscias* leaves. This suggests to us that more *Polyscias* was indicative of relative male experience as we consider males attempting to establish new sites or replacing traditional owners at their traditional sites to be younger birds (Frith & Frith, in press). In some cases where an unknown, unmarked, male took over the traditional court site of a traditional marked male at the start of a display season, we observed the presumed relatively inexperienced male to clear an inferior court and decorate it poorly. Such newly-acquired courts and their decoration improve over subsequent seasons. Thus, long established, older, court-

owning males used mostly *Polyscias* leaves whereas younger and/or peripheral males used less. Older males also selectively stole *Polyscias* leaves from courts of peripheral, probably subdominant, neighbouring males. These conclusions are supported by the findings of Borgia (1985a, 1986) who found the ability of male Satin Bowerbirds to build better quality bowers and retain greater numbers of decorations to be a function of age.

The more significant bower decorations of some other bowerbird species are items rare in the birds' environment (Borgia & Gore, 1986; Frith, 1989; Frith & Frith, 1990c) and it appears that an abundance of such decorations on bowers improves the owners mating success (Borgia, 1986). Rare decorations might, thus, indicate something significant to rival males and to females about fitness, and possibly level of dominance, of the males acquiring and retaining them. It is doubtful, however, that *Polyscias* leaves are rare in the Tooth-bill's present environment for in considering this possibility the modification or degradation of Tooth-bill habitat must be kept in mind. Pioneering *Polyscias* in our study area were characteristic of disturbed forest edge and gaps. Prior to any upland rainforest disturbance (i.e. roads, snig tracks, logging etc.) this plant would certainly have been less abundant and more patchily distributed than it is today. This aside, however, it is possible that *Polyscias* presents a leaf that has a structure and moisture content that gives a long 'court-life' and provides a strikingly contrasting pale underside.

We were unable to study male mating success relative to court position, size, or number of leaf decorations. We observed that a display tree, at or within the court periphery, is fundamentally important to enable males to initiate courtship by hiding from the female behind (Frith & Frith, 1993). Whilst all long-term traditional courts had at least one display tree a number of small and temporary courts, apparently made by younger males early or late in the display season, lacked such a tree. As the initial clearing of the court of all litter and debris doubtless involves considerable effort by, and cost to, the male and, given the observed variation in the size of area cleared it is possible that court size may be of some significance to females in mate selection. It should be noted that Grant & Laurance (1991) did not discuss court-size but unfortunately used the term 'court size' to represent the number of leaves on a court.

Of 54 courts examined for the presence of lawyer cane plants growing within them 37% proved to have them, indicating that this is not a prerequisite for a court location as suggested (Jackson, 1910). All fruit remains found on courts, often in discrete piles beneath favoured perches, are excreted by birds and not 'cast or vomited' as suggested by Jackson (1910).

LEAF TURNOVER RATES AND THEFT

Courts examined for leaf numbers, species and evidence of leaf stealing were those of part of the dense population of males on Tooth-bill Hill and adjacent slopes. These were traditional court-owners, which we concluded consisted of older and more experienced individuals. In most cases, colour-banding proved this to be true (Frith & Frith, in press).

Most leaves remained on courts for two weeks or less but some did so for up to three (dry season 79) or four (season 80) weeks, leaf turnover rates being faster with drier conditions. These results agree with Grant & Laurance (1991) who found most leaves were removed at 13 courts after two weeks or less. We found leaf turnover rates to be significantly higher during hotter drier periods of peak activity and, given that leaves are presumably selected for contrasting paler undersides, large size, flat structure and moisture retention (anti-curling properties), this is predictable as dehydration renders leaves unsuitable decorations more quickly. We performed no experiments on relative dehydration and deterioration rates of various leaf species, but observed that leaves of other species dried, curled and discoloured quicker than did *Polyscias*.

We found a peak activity court decoration rate of 5.9 and 6.8 and a removal rate of 7.3 and 6.4 leaves/day in seasons 79 and 80 respectively. These rates are higher than the 4.05 and 3.96 leaves added and removed per day respectively observed by Grant & Laurance (1991). Differences in leaf decoration and removal rates between individual males may reflect relative differences in experience, and/or dominance within the population of adjacent males. Grant & Laurance's (1991) period of study, however, included pre-peak activity, which would have lowered the overall rate of observed leaf replacement.

There were more leaves on courts during early peak activity in season 80 with a greater proportion of them *Polyscias*. Relatively fewer *Polyscias* leaves were present during later peak activity (and fewer still during post-peak activity), which

may suggest competition for favoured decorations is more intense initially each season, when males are establishing or re-establishing a social hierarchy. More leaf thefts occurred during early peak activity, indicating greater inter-male competition, and these mostly involved *Polyscias*.

Movement of stolen leaves among several adjacent well-established marked males' courts indicated the possibility of a social hierarchy. That one of nine adjacent individuals proved to steal more leaves from more adjacent courts than did all eight other birds combined, and apparently inhibited all other males from stealing from him (Fig. 5), is indicative of a system similar to that operating in some other polygynous bowerbird species (Borgia, 1985a,b; Borgia & Mueller, 1992). It is possible that more acquisitively successful court-owning males might obtain most successful matings within the localised dense population of court-owning males, or exploded lek (Frith & Frith, in press).

Borgia (1985a) demonstrated that male Satin Bowerbirds restrict their bower decoration theft raids to immediate neighbours, their most likely sexual competitors, as we do in the Tooth-bill (Fig. 5). He found, moreover, a highly significant correlation between male social dominance of individuals at feeding sites, and the number of bower destructions performed by the individuals, thereby providing evidence in support of bower interference being an aggressive act by which more dominant males can detrimentally affect the quality of bowers of rival males. We obtained no empirical data to support our hypothesis but we think it possible that a relatively large number of fresh and appropriate leaves on the court of a male, within an exploded lek, reflects that male's experience among the local male population and perhaps also his relative dominance.

MALE ATTENDANCE LEVELS AT COURTS

Over the peak court activity of season 79, 80 and 89 males spent an average of 64% of time attending courts. By radio-tagging four males, we and G. Moore showed that a bird was potentially present but silent high above his court where he might have otherwise been overlooked by an observer within a hide for up to 3% of total time. Differing court attendance levels by males during seasons 79, 80 and 89 clearly reflect seasonal environmental differences, being lowest during 79 (52%) and highest during 80 (79%). This pattern was the same during each month of peak activity and at different times of day.

The time that individual male Tooth-bills spent at courts during season 79 was lower and more variable than during 80 and 89. Males took longer absences from courts both during different months of peak activity and times of day in season 79, than 80 and 89. During 79, peak activity lasted only six weeks and it would appear that the dry conditions and poor fruit crop prevailing during this season were detrimental. The exceptionally dry early December of season 79 combined with a poor fruit crop caused birds to quit courts (Figs 3 & 6).

Court attendance levels by all males was high during season 80 and mean duration of absences from their courts was 3.7 and 2.2 times briefer than during seasons 79 and 89 respectively (Table 3) which would seem attributable to relatively greater availability of fruit (Fig. 3c). While the period of early peak activity of season 80 was relatively dry, fruit was prolific throughout the prolonged peak activity of 14 weeks. The onset of wet season rains terminated court attendance and, while significantly dry spells thereafter brought birds briefly back to courts, court attendance was low during post-peak activity (Table 4). Peak activity lasted ten weeks in season 89 with attendance levels being intermediate between those of 79 and 80 (Table 3). That the early 89 peak activity period was relatively dry, the November wet (Fig. 6), and the fruit crop relatively poor (Moore, 1991) possibly accounts for this.

Most polygynously-breeding passerines are inhabitants of tropical rainforests that eat predominantly, if not exclusively, fruits which are abundant in space and time in that habitat and require, therefore, a small proportion of the day to harvest. It has been argued that these ecological factors favour the evolution of polygyny because seasonally abundant fruit resources enable males to devote most of their time to courtship and females are able to provision their offspring unaided by the promiscuous males (Snow, 1976, 1982; Snow & Snow, 1988; Beehler, 1989).

Male Tooth-bills are almost exclusively frugivorous during their courtship and mating season (Frith & Frith, unpubl. data) and while nesting females are known to also feed insects to their young, the diet of the offspring is probably predominantly fruit (Frith & Frith, 1985a). Thus, this bowerbird fits well the ecological scenario common to most polygynous passerines. In the case of some neotropical polygynous passerines, males have been observed to spend as much as 87-90% of daylight hours attending display

courts or perches (Snow & Snow, 1988). It is most noteworthy, therefore, that male Tooth-bills appear far more frugivorous than males of other bowerbird species and spend significantly longer at their courts than do males of other bowerbirds. This was emphasised because during this study, male Tooth-bills spent significantly longer at their courts during the season of highest fruit abundance.

Male Satin Bowerbirds, a species with a 67% fruit component of annual diet, spent an average of 73% of daytime within 50m of their bowers (Donaghey, 1981). Males of the predominantly frugivorous Macgregor's Bowerbird *Amblyornis macgregoriae* spent 54% of daylight at, or within 20m of, their bowers (Pruett-Jones & Pruett-Jones, 1982, 1985). A male Great Bowerbird, a species considered to be predominantly frugivorous (Diamond, 1986; Schodde & Tidemann, 1988) spent 47% of daylight hours at or near his bower (Veselovsky, 1978). The Regent Bowerbird's annual diet includes 81% fruit and yet males were found to spend a mere 3% of daytime at or near their bowers. The explanation for this exception is that regent bowerbirds *Sericulus* species represent an early stage in the evolution of bower-building, in which bowers have not yet replaced elaborate male nuptial plumage. Male Regent Bowerbirds *S. chrysocephalus* initiate courtship in the forest canopy before accompanying the female to the bower where a prolonged courtship display primarily presents colourful nuptial plumage, not the bower, to the female (Lenz, 1993).

MALE BEHAVIOUR AT COURTS

The length of time males spent at courts at each visit was similar for individual males during each season, different months of peak activity and at different times of the day (Tables 3-5). Once males started to attend courts the proportion of time they spent giving advertisement song, performing court maintenance or displaying was similar each season (Tables 6-8). Of their time at courts males invested 95.7% in performing loud advertisement song from favoured perches, 2.4% in silence, 1.2% in court maintenance and 0.7% in display.

Most (99%) advertisement song was performed by male Tooth-bills from favoured high, adjacent or court perches, males rarely singing on the ground prior to display subsong. Birds spent more time singing on high and adjacent perches during the drier and hotter 79 season than in 80 and spent more time on higher perches during the brighter

and hotter time of day. During season 80, males spent more time on court perches as the season progressed. Most birds frequented only one or two, favoured, adjacent court perches, resulting in large accumulations of excreted fruit remains beneath them.

Male Tooth-bills spent a mean of 1.4mins maintaining courts. Given that males were present immediately above their courts for 64% of total time, the 1.2% of time spent in court maintenance is remarkably brief compared with mean proportion of time spent in bower maintenance by Macgregor's Bowerbirds (12%; Pruett-Jones & Pruett-Jones, 1982), Satin Bowerbirds (8%; Donaghey, 1981), Great Bowerbirds (Veselovsky, 1978), Western Bowerbirds *C. guttata* (Bradley, 1987) Spotted Bowerbirds *C. maculata*, Fawn-breasted Bowerbirds *C. cerviniventris* and Lauterbach's Bowerbirds *C. lauterbachii* (Frith & Frith, 1989, unpubl. data). It is similar, however, to that invested by the Regent Bowerbird which builds the most rudimentary and sparsely decorated of bowers (Lenz, 1993).

Male Tooth-bills do not spend much time on the court 'searching for insects and snails' as reported by Forshaw (in Cooper & Forshaw, 1977). The limited time they did spend on the cleared court area presumably merely reflects the low maintenance required once it is initially cleared and decorated. The cryptic morphology of males, their habit of remaining all but motionless when perched, of being silent when maintaining the court, the ventriloquistic quality of their calls, the extreme brevity of their courtship display (Frith & Frith, 1993), the adoption of a sleeked frozen posture when alarmed and the fact that they are not infrequently preyed on at their courts by goshawks *Accipiter* spp. (Frith & Frith, unpubl. data) all suggest that predation might have significantly influenced some or all of this behaviour. The fact that we witnessed not a single aggressive encounter between birds at a court other than owning birds chasing off another suggests such events are extremely rare.

MALE VOCALISATIONS AT COURTS

Bower-attending bowerbirds studied to date advertise the bower location with specific calls given relatively infrequently (Gilliard, 1969; Cooper & Forshaw, 1977; Veselovsky, 1978; Donaghey, 1981; Frith & Frith, unpubl. data) and use a distinctly different, usually quieter and more complex, song in courtship display that in the case of the Satin Bowerbird (Loffredo & Borgia, 1986), the Regent Bowerbird (Lenz,

1993) and gardener bowerbirds *Amblyornis* spp. (Frith & Frith, 1993, Frith & Frith, unpubl. data) often includes avian mimicry. Tooth-bill, Satin, Macgregor's, Streaked Bowerbird *Amblyornis subalaris* and Archbold's Bowerbird *Archboldia papuensis* calls lack directional cues or have ventriloquistic qualities (Frith & Frith, unpubl. data). It has been suggested that this is a result of the enhanced risk of predation upon birds calling from long-term traditional locations (Robinson, 1974).

Advertisement song of Tooth-bills consisted of seven component calls. Phases of several to all of these calls were performed during each visit and usually followed a definite sequence. Thus males returning to courts invariably first gave a 'chuck', as noted by Chaffer (1984), or less frequently a squeal. 'Chuck' and 'squeal' calls were followed by 'chuck + babble' or 'chuck + mimicry'. These were followed by 'babble', 'babble + mimicry' and/or 'mimicry'. Display vocalisations (Frith & Frith, 1993) usually followed the latter three calls. Sometimes, but not often, the sequence of calls was broken when males changed position on a, or moved to another, perch. In these instances they often gave 'chuck' calls again. The 'chuck' appeared to us the loudest, most far-carrying, and most locatable call. This may explain why 'chuck' is used to recommence calling, as it clearly and quickly establishes the bird's presence and location. It is possible the 'chuck', which we here treat as a natural Tooth-bill call, is in fact mimicry of a similar note of Bower's Shrike Thrush, particularly as calls of this species dominated Tooth-bill mimicry. Of the total time males spent advertisement singing at their courts, at least 60% of vocalisations included elements of mimicry (Table 10).

Calling male Tooth-bills at locations remote from Paluma sound similar in general terms but incorporate some different avian model species into their mimicry and/or give different bias to different species (C. & D. Frith, unpubl. data) as is found in Satin Bowerbirds (Loffredo & Borgia, 1986) and lyrebirds *Menura* spp. (Smith, 1988) at different areas. This is indicative of the kind of 'culturally' transmitted behavior seen expressed in the bower architecture and decorations of bowers of geographically distinct populations of bowerbird species (Diamond, 1986, 1987).

While the loud song of the Tooth-bill presumably functions to indicate presence to rival males (Marshall, 1950) we think the conspicuous mimicry content may function to advertise court location and bird status to females (see below).

Once a female shows serious interest in the court the male Tooth-bill performs a far softer 'subsung' exclusively of mimicry (Frith & Frith, 1993), as do male Satin Bowerbirds and Noisy Scrub-birds *Atrichornis clamosus* (Loffredo & Borgia, 1986; Robinson, 1974). We think it likely that this subsong is in fact more informative to females than advertisement song as it has been demonstrated that female Satin Bowerbirds use the quality of more intimate male mimicry to assess the relative merits of prospective mates (Loffredo & Borgia, 1986). Contrary to Robinson (1974), but consistent with Dobkin's (1979) interpretation that male bowerbird mimicry is given in precopulatory display (and in nest defence by females), the male Tooth-bill does specifically perform mimicry prior to and during courtship displays, as male Satin Bowerbirds appear to do (Loffredo & Borgia, 1986).

Loffredo & Borgia (1986) showed that among competing male Satin Bowerbirds, older males produced longer bouts of higher-quality avian vocal mimicry than younger males and as a consequence gained higher mating success. These authors also found that the male Satin Bowerbirds in their study area performed mimicry of only two bird species during courtship and that when both were given they were always performed in the same order. During subsong mimicry male Tooth-bills showed a strong tendency to perform their repertoire of approximately ten model species and other sounds in a particular order and within a minute (Frith & Frith, 1993).

The nature of male Tooth-bill vocalisations would suggest that females may make some general assessment of male experience from their loud court advertisement song prior to selecting individual males and/or songs for visitations. This initial loud 'broadcasting' of mimicry may reflect pressures of greater male competitor density. During the subsequent court visit females can assess the quantity and quality of the more stereotyped sub-song exclusively of mimicry (Frith & Frith, 1993). Thorpe (1985) stated that there is some evidence that variety in male bird song is attractive to females, and suggested that mimicry may simply be a way of increasing repertoire size.

The repertoire of singing male court owners was found to change, by other bird calls being opportunistically mimicked, thus incorporating novel characters into the song. Bourke & Austin (1947) also noted that males would stop calling to listen to other bird species and then immediately mimic the bird listened to. Goodwin (1986)

reported several wild Jays *Corvus glaucurus* mimicking the call of the Grey Heron *Ardea cinerea* immediately upon seeing this species. Smith (1988) observed the same behaviour by mimicking, promiscuous male, lyrebirds. The significance of such individualistic call components is unknown. The idea that females may in fact select for novel secondary sexual characteristics has, however, recently been presented (Ten Cate & Bateson, 1988; Christidis & Schodde, 1993). It is possible this theory may have significance to the question of avian mimicry in addition to the finding of Loffredo & Borgia (1986) that male Satin Bowerbirds performing more and better mimicry were older individuals obtaining higher mating success.

Hoglund (1989) observed that in lekking birds all species that display on the ground have larger males than females, with the exception of the Great Snipe *Gallinago media*. He noted that the male Great Snipe uses vocalisations rather than nuptial plumage to enhance reproductive success. It is noteworthy, therefore, that the terrestrially-displaying Tooth-bill is cryptically monomorphic in plumage, nearly so in size, and that males use prolonged complex vocalisations but a markedly brief display (Frith & Frith, 1993) in courtship. Five adult male Macgregor's Bowerbirds, decorated only with an extensive orange crest, spent an average of 71% of court attendance time perched silently and 14% vocalising from traditional perches (Pruett-Jones & Pruett-Jones, 1982). Brilliantly-plumaged adult male Regent Bowerbirds spent a mere 1.01% of their total, brief, court attendance time vocalising (Lenz, 1993).

It is possible, therefore, that continuous loud complex vocalisations by male Tooth-bills, at least in part, compensates for the lack of visual secondary sexual characters by containing information that rival males and potential mates can use to assess male 'fitness'. It has been noted that in the evolutionarily convergent polygynous Cotingas (Passeriformes, Cotingidae) of the Neotropics, in which most species are conspicuously sexually dimorphic, the lekking males of the few species with much-reduced or no sexual dimorphism use vocal behaviour to attract and court females far more than their relatives. (Snow 1982). Male Tooth-bill fitness could be indicated by the amount of calling (time invested at the court) and/or its qualities and proportion of avian mimicry (reflecting male experience). Loffredo & Borgia (1986) found that female Satin Bowerbirds use male vocalisations, particularly

the quality of mimicked bird calls, as an indication of relative male age. They found that older males perform better mimicry and that females selected for the ability in males to learn complicated songs.

Thus, while female Tooth-bills cannot simultaneously compare members of an 'exploded' aggregation (lek) of males displaying their vigor and plumage (as females in true leks can) they may be able to simultaneously assess court attendance levels as indicated by vocalization time and the quality of song content. By this means females could initially assess male age (cf. Loffredo & Borgia, 1986) from perches above or adjacent to areas of greater court densities that in effect form exploded leks (Frith & Frith, in press), prior to selecting a male(s) to visit.

ACKNOWLEDGEMENTS

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A NEW FRESHWATER BIVALVE FROM THE TRIASSIC OF SOUTHEASTERN QUEENSLAND. *Memoirs of the Queensland Museum* 37 (1):146, 1994:- Collections made from the Blackstone Formation, Ipswich Coal Measures, have yielded, *Protovirgus clellandi* sp. nov. in addition to bivalves reported by Etheridge (1892), McMichael (1957), and Hill et al. (1965). *P. clellandi* sp. nov. is also reported from the Tingalpa Formation. A Late Triassic (Carnian) age has been ascribed to the Blackstone Formation by de Jersey (1975), and the Tingalpa Formation (de Jersey & Hamilton, 1965).

Class BIVALVIA Linne, 1758

Order UNIOIDA Stoliczka, 1871

Family UNIONIDAE Fleming, 1828

Protovirgus McMichael, 1956

Protovirgus clellandi sp. nov.

Material. Holotype: QMF29473, from mullock heaps at Ebbw Vale, which are derived from the Blackstone Formation, Claypave Quarry, Dinmore. Paratypes: QMF29475, QMF32226, same data as holotype; QMF27523, from road cutting on Gateway Arterial road, Brisbane, Tingalpa Formation.

Diagnosis. Medium sized, equivalved, elongate unioid with inflated umbonal area and fine comarginal ornament. Hinge straight and long. Tapering strongly to the posterior. Ventral margin is sharp. Dentition unknown. Anterior adductor scars are raised on platforms near the umbones.

Description. Maximum height ranges from 28-39mm, width 27-36mm and in length 75-123mm (Table 1). Height and width is approximately equal along the shell length. Hinge straight, the ligament is apparently wide and extends approximately 2/3 of the shell length. Umbones anterior, placed at no more than 1/6 of shell length. Strongly tapering posteriorly, shell is apparently thin with ornament of fine growth lines. Rounded at posterior margin. Anterior adductor scar just ventral of umbo consists of slightly raised platform with 3 or 4 small slightly ovate pits. Posterior muscle scar unknown. Dentition unknown.

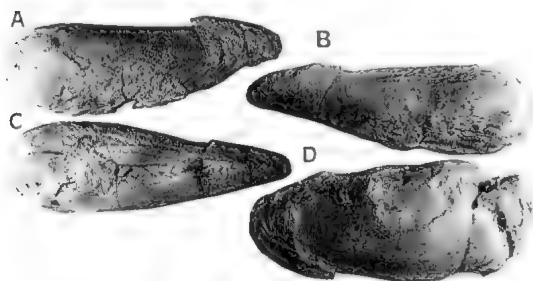


FIG. 1. *Protovirgus clellandi* sp. nov. A-C, QMF29473, x0.3. A, left valve; B, right valve; C, dorsal view. D, paratype, QMF29475, right valve x0.5.

TABLE 1. Morphometric data for specimens of *Protovirgus clellandi* sp. nov. from the Blackstone and Tingalpa Formations. Measurements in mm.

| Specimen | Height | Length | Width |
|----------|--------|--------|-------|
| QMF29473 | 39 | 123 | 36 |
| QMF29475 | 31 | 75 | 27 |

Remarks. The tapering form, rounded posterior end, sharp ventral margin and strongly anterior umbones ally the present material with *Protovirgus* McMichael, 1956. The type species, *P. dunstani* (Etheridge Jr., 1888 described by McMichael 1956: 232, fig. 8) from the Triassic of New South Wales is much smaller and less robust than *P. clellandi*. *P. flemingi* McMichael (1956: 232-233, figs 1-3) from Cretaceous of New Zealand is also smaller and the umbones are less anteriorly placed. *P. jaenschi* Ludbrook, 1961 from Triassic strata at Leigh Creek, South Australia has a greater height to length ratio, and is more gently tapering than *P. clellandi*. *P. coatsi* Ludbrook, 1961 is smaller and does not taper as strongly as *P. clellandi*, resulting in a far more ovate outline.

Etymology. For John Clelland Hocknull.

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- Scott A. Hocknull, *Queensland Museum PO Box 3300, South Brisbane, Queensland 4101, Australia; 10 August 1994.*

HOME RANGE AND EXTRA-COURT ACTIVITY IN THE MALE TOOTH-BILLED BOWERBIRD, *SCENOPOEETES DENTIROSTRIS* (PTILONORHYNCHIDAE).

CLIFFORD B. FRITH, DAWN W. FRITH AND GEOFFREY J. MOORE

Frith, C. B., Frith, D. W. & Moore, G. J. 1994 12 01: Home range and extra-court activity in the male Tooth-billed Bowerbird *Scenopoeetes dentirostris* (Ptilonorhynchidae). *Memoirs of the Queensland Museum* 37(1):147-154. Brisbane. ISSN 0079-8835

Home range, time utilisation and activities of four male Tooth-billed Bowerbirds away from their adjacent courts were monitored by radio-tracking throughout the 1989 display season in upland rainforest of north Queensland. Three of the males were known to be adults, having attended their courts for ten or more seasons. Males spent an average of 36% of their time absent from courts during peak display season activity. The mean home range of males was 9.5ha, with a mean overlap of 50%. Median distances travelled by males from their courts for all activities ranged from 40-86m, with a maximum range of 311-391m. Activities away from courts included foraging, collection of leaf decorations directly from trees or by theft from neighbouring courts, interactions with conspecifics, bathing and drinking. Most absences (60%) were primarily for foraging which represented 83% of total time absent with a mean duration of 18mins per absence. Some 18% of absences, representing 7% of total time absent, involved exclusive non-foraging activities. Almost all of these absences were brief with a mean duration of 5 mins. The remaining 22% of absences, representing 10% of total time absent, from the court involved unknown activities. Absences from courts were shortest during November, and during the early part of the morning (0600-0900h). The implications of these data are discussed. □ *Tooth-billed Bowerbird home range size, time utilisation and activities away from courts, Ptilonorhynchidae, Australia.*

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Several families of passerine birds include species that exhibit polygynous mating systems in which promiscuous, competitive and often ornate males take no part in nest duties. In most of these species males spend much of the day at either solitary or communal (lek) display perches; females are attracted to these sites by the calls of the males and are courted by a variety of displays (Gilliard, 1969; Snow, 1982; Beehler & Pruett-Jones, 1983, Beehler 1989). The Tooth-billed Bowerbird, *Scenopoeetes dentirostris* is one such species (Frith & Frith, 1985, 1993). Males of this species establish cleared courts on the forest floor in areas of suitable topography; mean nearest neighbour distances in these areas are 50m (Frith & Frith, in press). Frith and Frith (1994) found that during peak activity male Tooth-bills spent an average of 64% of the day (0600-1800h) at courts; court visits averaged 23mins and court absences averaged 14mins. The birds spent more time at their courts during seasons of greater fruit abundance.

The behaviour of male Tooth-bills at courts is increasingly well understood (Frith & Frith, 1993, 1994; in press). However, nothing is known

about home range size, time utilisation and activities of male Tooth-bills away from their courts. This paper reports observations on the behaviour and movement of four court-owning male Tooth-bills using radio-tracking and simultaneous observation from hides near courts. The aims of this work were threefold: to identify the role of male Tooth-bills as seed dispersers within tropical rainforest (Moore, 1991); to determine whether male Tooth-bills spent much time present, but silent, in the canopy above or within the vicinity of their court (Frith & Frith 1994); and to ascertain home ranges and activities of males away from the courts. The third aim is the subject of the present paper.

STUDY AREA AND METHODS

The study area comprised 50ha of upland tropical rainforest, altitude c.875m, on the Paluma Range (19°00'S, 146°10'E), north-eastern Queensland, 7km from Paluma Township, 80km north of Townsville. Descriptions of the Paluma Range study area and its climate appear in Frith and Frith (1994). Half of the site was divided into permanently marked 25 × 25m grid squares and

the remainder was divided into 25 × 50m rectangles; this enabled accurate plotting of locations at which the birds were observed.

Radio-tracking was undertaken during the 1989 display season (17-27 October, 16-26 November and 12-22 December). Four males (from courts 23, 33, 35, 37; Frith & Frith, 1994: fig. 1) were caught in mist nets near their courts and were banded with a metal band and a unique two colour-band combination. Males at courts 23 and 37 had been the traditional owners at those sites for ten previous display seasons and the male at court 35 for 11 previous seasons. The male at site 33 was unbanded at the start of the 89 display season and may have been the unmarked owner of this site for the two previous seasons.

Each male was monitored for four periods (0600-0900, 0900-1200, 1200-1500, 1500-1800h) during October, but only three males were monitored during November (at sites 23, 35, 37) and December (23, 33, 37). All males were radio-tracked for a total of 120 hours. The first hour of the first tracking period (at site 33) was excluded from the analysis due to possible disturbance (see below). Male 37 lost a transmitter during one tracking period and, although his court arrivals and departures were recorded, his activities away from the court were unknown. Radio-tracking was also carried out after 2000h, for two 30 minute periods at each court, to ascertain whether the owner roosted above his court.

Each male was fitted with a 4g Biotrack single stage radio-transmitter (SS-1) using a tail mount (Kenward, 1978). Radio-tagged individuals were readily identified by the antenna extending beyond the tail. To assist rapid identification of individuals when they were in the canopy a small amount of contrasting-coloured paint was placed on the underside tips of the outer tail feathers. Radio-tracking was initiated a week after capture to allow sufficient time for the birds to adjust to the transmitter.

We established cryptic canvas hides six metres from each court two weeks before starting the study. The observer (DWF) remained within the hide during each tracking period and all bird behaviour, locations, departure and return times and flight directions were noted. Each three hour observation period was started either ten minutes after establishing DWF in the hide or earlier if the male returned to his court and behaved normally. The observer was in constant radio contact with the radio-tracking team and alerted them as soon as a bird left or arrived at his court.

The radio-tracking team remained at least 30m distant from the courts of the radio-tagged birds to minimize disturbance to the court owner or to other Tooth-bills in the area. The tracking team consisted of GJM, with the radio antenna and receiver, who followed the bird's signal and marked destinations, and CBF who attempted to maintain visual contact with the bird and informed GJM of its location and behaviour in the canopy and of the compass bearing of signals.

Males were tracked using a Telonics (U.S.A.) Tr-2 receiver. To improve reception at close range and direction finding ability, an enhanced manual gain control was fitted to the receiver. A three element, folding hand held Yagi antenna (Custom Electronics, U.S.A.) was used for direction finding. Use of a small single earphone assisted communication between observer and tracker; this was necessary because many forays resulted in a dash of up to 400m to determine the bird's destination.

Once a male had been followed to a destination, the tree was tagged and, at a later date, the positions of all destination trees were mapped in relation to the pre-established grid. On a few occasions males flew beyond the limits of the study site; in these cases the locations of destination trees were plotted by tape and compass.

Signal strength and consistency were used as a guide to bird activity and if the bird could not be sighted, its position was determined by triangulation. If the signal was strong and consistent, this usually meant the bird was stationary. A bearing was then taken from the nearest grid reference point and a second bearing taken at the next grid reference point to obtain a fix. To test the accuracy of this method, calibration transmitters were placed in trees and the resulting fixes were found to be within 5m of the actual transmitter position.

A highly variable signal, in both strength and consistency, indicated the bird was moving. In these cases the signal was followed until a strong and consistent signal was obtained and the process was then repeated. If foraging, a strong variable signal was obtained as the bird would change its orientation while moving between branches. The sound of falling debris or fruit was often a good indicator of approximate bird location within the forest canopy. If interacting with other individuals, calls and chase flights were often heard.

Establishing a final destination using radio-assisted surveillance usually resulted in tracker and observer reaching a destination some time after

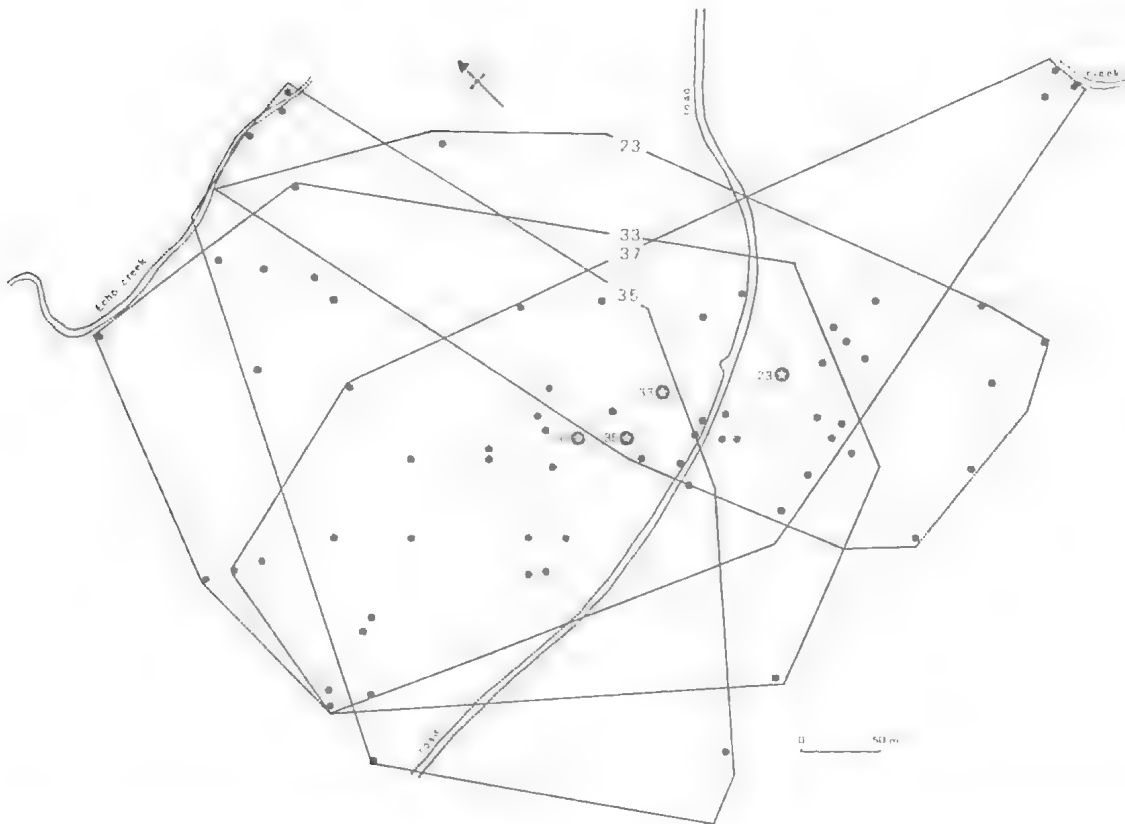


FIG. 1. Minimum Convex Polygon home range areas ($n = 636$ fixes*) for four male Tooth-billed Bowerbirds, based upon their adjacent courts, during the 1989 display season. Numbered stars = male's court location and number. Solid dots = sightings of males in tree canopy. * male 23 = 202 fixes; 33 = 148 fixes; 35 = 122 fixes; 37 = 164.

the bird. This problem increased the further the male travelled from his court. In addition, male Tooth-bills are well camouflaged and rely on cryptic habits to avoid predation (Frith & Frith, 1993, 1994). For these reasons it was often difficult and sometimes impossible to establish either the final destination or the activities of a bird, leaving the reason for many forays by a bird as unknown, and destinations as approximate areas only.

In this paper absences from courts are classed broadly as foraging, non-foraging and unknown activities. Foraging absences were those primarily concerned with visits to food trees where fruits were eaten but sometimes brief non-foraging activities were observed before or after feeding. Non-foraging absences did not include visits to fruiting trees or, to the best of our knowledge, feeding. Foraging and non-foraging activities

were either observed directly or inferred from characteristics of the destination of the bird, the radio signal or sounds from the canopy. Direct return flights from a destination tree to a court were determined by the rapid loss of a signal and the subsequent recording of the male at the court by DWF in the hide.

Many home range estimators are available for home range analysis (Mohr, 1947; Southwood, 1978; Anderson, 1982; Worton, 1989). Following animals using focal sampling results in autocorrelation of locations (i.e. non-independent fixes). This may create problems in the analysis of radio-tracking data. However, several recent studies have found that home range estimates based on independent versus non-independent locations are statistically indistinguishable (Anderson & Rongstad, 1989; Gese et al., 1990). As most fixes obtained during this study were

TABLE 1. Three-way fixed factor Analysis of Variance * examining the effect of month, time period and individual male on home range estimates for four male Tooth-billed Bowerbirds during peak activity of the 1989 display season.

| Treatment | df | F | P |
|--|----|------|-------|
| Month | 2 | 1.43 | 0.269 |
| Time period | 3 | 1.26 | 0.320 |
| Individual male | 3 | 2.31 | 0.115 |
| Month \times Time period | 6 | 0.22 | 0.965 |
| Time period \times Month | 9 | 0.38 | 0.938 |
| Month \times Time period \times Bird | 18 | | |
| Total | 39 | | |

* = values obtained using Minimum Convex Polygon method

non-random the Minimum Convex Polygon (Mohr, 1947; Southwood, 1978) estimator was used to estimate home range size. This method is sufficiently robust to deal with non-independence of locations. Home range and home range overlap were estimated using the commercial package Ranges IV.

Most frequency distributions of time and space use about a court by the male owner were highly skewed towards the court; therefore the median was chosen as the best indicator of the central place tendency of the data, rather than mean (Zar, 1979).

RESULTS

HOME RANGE

The mean home range area for four male Tooth-bills over the 1989 display season was 9.5ha (range 6.9-12.5) as determined from a total of 636 fixes obtained away from courts (Fig. 1). In a three way fixed factor analysis of variance examining the effect of month, daytime period and individual on the home range estimate, there were no significant differences (Table 1). Mean overlap of the four home ranges was 50% with a range from 23-80% (Fig. 1, Table 2). There was a significant difference in the amount of overlap observed between individual males and their nearest neighbours (one way Analysis of

TABLE 2. Percent overlap of the home ranges of four radio-tagged male Tooth-billed Bowerbirds away from their courts during peak activity of the 1989 display season.

| Male | 23 | 33 | 35 | 37 |
|------|------|------|------|------|
| 23 | - | 26.0 | 32.4 | 45.1 |
| 33 | 50.7 | - | 64.3 | 54.7 |
| 35 | 22.6 | 78.6 | - | 47.7 |
| 37 | 34.6 | 78.6 | 38.2 | - |

Variance using arcsin square root transformed proportions: $F = 6.36$, $df = 3$, $P = 0.0164$). The greatest home range overlap was observed between males whose courts were closest together (Fig. 1, Table 2).

The median distance males travelled from their courts for all activities was 59m, with a minimum of 8m and maximum of 391m (Table 3). Minimum distances occurred when males stole leaf decorations from a neighbour's court or chased off conspecifics at short distance from their own court. Maximum distances occurred when males flew to a creek to bathe, usually in the middle of the day. The nearest significant body of water was located in a gully about 300m from the courts (Fig. 1).

TIME UTILISATION

Males spent an average of 64% (range 56-73%) of total time (0600-1800h) attending courts during peak activity of the 1989 display season. Up to 3% of this time present males were detected above their courts by radio signals, but remained unseen or unheard by the observer in the court hide (see Frith & Frith 1994: table 3). In a three way fixed factor analysis of variance examining the effects of month, daytime period and individual male on the proportion of time spent at the court during 1989, there were no significant differences (Table 4). Court attendance levels and time-budgeted activities at courts by the four males during different months (October-December) and during different times (0600-1800h) of the day during this season are reported elsewhere (Frith & Frith, 1994). The results of radio-tracking at courts at night revealed that each male Tooth-bill roosted above his court.

Males spent an average of 36% (range 27-44%) of total time (0600-1800h) absent from their courts during peak activity of the 1989 display season, with a mean duration per absence of

TABLE 3. Distances (m) of all movements away from courts by four male Tooth-billed Bowerbirds during peak activity of the 1989 display season.

| Male | Number of fixes | Median distance | Minimum distance | Maximum distance |
|-------|-----------------|-----------------|------------------|------------------|
| 23 | 202 | 50.6 | 27.2 | 354.8 |
| 33 | 148 | 58.6 | 13.9 | 370.7 |
| 35 | 122 | 66.4 | 14.3 | 311.2 |
| 37 | 164 | 40.4 | 8.2 | 391.4 |
| Total | 636 | 59.4 | 8.2 | 391.4 |

TABLE 4. Three-way fixed factor Analysis of Variance * examining the effect of month, time period and individual male on proportion of time four male Tooth-billed Bowerbirds spent at their courts during peak activity of the 1989 display season.

| Treatment | df | F | P |
|--|----|------|--------|
| Month | 2 | 0.51 | 0.6091 |
| Time period | 3 | 0.12 | 0.9494 |
| Individual male | 3 | 1.06 | 0.3918 |
| Month \times Time period | 6 | 0.21 | 0.9700 |
| Time period \times Month | 9 | 0.21 | 0.9885 |
| Month \times Time period \times Bird | 16 | | |
| Total | 39 | | |

* = using arcsin square root transformed proportion data.

13.1mins (range 8.4-17.7). The proportion of total time males were absent and the mean duration of absences were lower during November than during October or December. Males spent less time at courts during the middle of the day between 0900-1500h (Table 5).

During the first hour (0600-0700h) of the first October tracking period male 33 cleared a small subsidiary court some 40m away from his primary one. Because this unusual behaviour may have been caused by banding, transmitter attachment or both the records from this hour have been excluded from analyses. During subsequent October tracking periods this male occasionally flew over, and perched briefly above, the rudimentary court (<3% of total time absent from his established court). Male 33 spent more time absent from his court than the other three males and Male 37 spent less time absent (Table 5), but differences between the four males were not significant ($\chi^2 = 3.78$, $P > 0.02$).

TABLE 5. Activities performed by four individual male Tooth-billed Bowerbirds during absences from their courts over peak activity of display season.

| ABSENCES: | | FORAGING | | | NON-FORAGING | | | UNKNOWN ACTIVITIES | | | TOTAL | | |
|----------------|-------------------------|--------------------|------------------|---------------------|--------------------|------------------|---------------------|--------------------|------------------|---------------------|--------------------|------------------------|---------------------|
| Male | Hours of radio-tracking | Number of absences | % of time absent | Mean mins @ absence | Number of absences | % of time absent | Mean mins @ absence | Number of absences | % of time absent | Mean mins @ absence | Number of absences | % of total time absent | Mean mins @ absence |
| Male | | | | | | | | | | | | | |
| 23 | 36 | 43 | 64.6 | 16.1 | 5 | 7.9 | 13.0 | 12 | 7.5 | 5.1 | 60 | 13.6 | 37.6 |
| 33 | 23 | 26 | 60.8 | 21.2 | 5 | 3.7 | 4.6 | 5 | 5.5 | 6.8 | 36 | 16.9 | 44.1 |
| 35 | 24 | 21 | 69.8 | 24.0 | 7 | 5.2 | 5.1 | 4 | 4.0 | 5.6 | 32 | 17.7 | 39.2 |
| 37 | 36 | 29 | 65.3 | 13.1 | 16 | 8.6 | 2.9 | 22 | 25.9 | 6.8 | 66 | 6.4 | 27.6 |
| Month | | | | | | | | | | | | | |
| October | 47 | 39 | 60.8 | 19.9 | 15 | 8.9 | 4.7 | 16 | 10.8 | 6.8 | 72 | 13.4 | 34.1 |
| November | 36 | 35 | 76.4 | 13.9 | 13 | 9.0 | 4.2 | 16 | 12.5 | 4.9 | 64 | 9.7 | 28.6 |
| December | 36 | 45 | 67.5 | 19.3 | 4 | 3.5 | 6.8 | 12 | 9.0 | 7.6 | 61 | 16.3 | 49.0 |
| Time | | | | | | | | | | | | | |
| 0600-0900 | 29 | 32 | 76.5 | 11.4 | 16 | 10.3 | 3.1 | 10 | 13.2 | 5.3 | 58 | 8.2 | 27.4 |
| 0900-1200 | 30 | 28 | 65.1 | 22.0 | 4 | 3.4 | 6.1 | 13 | 11.5 | 6.4 | 46 | 16.1 | 40.1 |
| 1200-1500 | 30 | 29 | 60.1 | 20.9 | 6 | 8.3 | 10.5 | 15 | 11.3 | 5.7 | 60 | 15.1 | 41.9 |
| 1500-1800 | 30 | 30 | 77.8 | 18.2 | 5 | 5.2 | 4.3 | 5 | 6.1 | 7.6 | 44 | 14.1 | 34.6 |
| Total/means/SE | 119 | 119 | 62.8 | 17.9 | 35 | 6.6 | 5.0 | 43 | 10.4 | 6.3 | 197 | 13.1 | 39.6 |

ACTIVITIES AWAY FROM COURTS

Of 197 total absences from courts 119 were foraging absences (60%), 35 non-foraging absences (18%) and 43 absences with unknown activities (22%), representing 82.8, 6.8 and 10.4% of total time absent respectively (Table 5). A foraging absence averaged 17.9mins (range 11.4-24), a non-foraging absence averaged 5mins (range 2.9-13) and an absence with unknown activities 6.3mins (range 5.1-6.9,

Table 5).

During foraging absences the birds were seen in destination food trees for 67% of the time; the remaining time being spent en route to or from the court (30%) or performing non-foraging activities (3%). Sixty six of the 119 foraging absences were to known food trees. The median foraging distances travelled by three males to these trees ranged from 19-42m, but male 37 flew much further to forage, with a median distance of 119m.

During a foraging absence males usually flew directly from the court to a food tree. On eight occasions, however, a court-owning male chased a conspecific from his court before continuing on to a food tree (see below). Males also occasionally flew directly towards a creek (before or after feeding) where it was assumed they went to bathe or drink, but trackers were only able to visually confirm this twice. Most times (86% of foraging absences) the bird flew directly back to the court

but on 15 occasions (14% of foraging absences) a leaf decoration was collected during the return trip. It is possible that undetected activities occurred during flights between courts and food trees.

Of the 35 non-foraging absences 12 entailed collection of a leaf decoration from a tree (3 leaves) or from another court (9 leaves), 12 were visits to the forest canopy above a neighbouring court, and 11 involved the male court-owner chasing a conspecific and then returning immediately to his own court (see below). Theft involved a male flying directly to a neighbouring court, quickly and quietly stealing a leaf from it, and returning directly to his own court. Leaf theft represented 0.5% of total time absent from the court, with a mean duration of 1.5mins per theft. The 12 visits to a neighbouring court were brief and involved the court-owner flying directly to, and perching quietly above, his neighbour's court for a short period (mean duration = 3.3mins), possibly with the intention of stealing a leaf. This behaviour was performed by all four males.

Males were seen to chase conspecifics away from the court on 19 occasions flying on to a food tree after eight such chases and returning directly back to the court after 11 of them. Three chases were in pursuit of a presumed female (having previously been displayed to). It is possible other chases were after a neighbouring male. On one occasion a leaf was stolen by a marked, neighbouring male just as Male 37 returned to his court. The latter male immediately chased the thief to the thief's court, about 70m away, where he stayed briefly before returning to his own court without a leaf. He was, however, subsequently seen to steal from that particular neighbour's court.

Interactions between conspecifics were observed away from the court. On four occasions a male left his court and flew to where other Tooth-bills were heard displaying, either above or on another court. On one occasion Male 35 was seen calling and displaying to an assumed female near a creek that was about 300m from his court. On two occasions two birds were seen facing each other in a food tree, face to face, with conspicuously sleeked plumage and agitated vocalisations.

DISCUSSION

Beehler & Pruett-Jones (1983) reviewed available information concerning the spatial dispersion of adult males of nine polygynous bird of paradise species (Paradisaeidae) from New

Guinea rainforests. These species were known or presumed to involve promiscuous males. Males of species with a predominantly arthropod diet were found to be territorial while males of predominant frugivorous species were non-territorial. Lack of territoriality in predominantly frugivorous passerine species is considered to result from the fact that tropical fruits are economically undefendable (Lill, 1976; Beehler, 1989; Beehler & Pruett-Jones, 1983).

During the 1989 display season the mean home range size of male Tooth-bills was 9.5ha and the median distance travelled from courts for all activities was 59m. Comparable data on the breeding season home range of other tropical frugivorous birds which display at focal sites are scarce. Pruett-Jones & Pruett-Jones (1988) reported that the home range of one adult male Blue Bird of Paradise, *Paradisaea rudolphi*, was 4.7ha over the season, about half the size observed in male Tooth-bills. Display trees of the former species are much more widely spaced than are the courts of Tooth-bills (220m vs 50m respectively). Blue Birds of Paradise are not as exclusively frugivorous through the breeding season as are Tooth-bills (cf. Beehler & Pruett-Jones, 1983) and this, together with a possible greater abundance of food near display sites, may account for differences in home range sizes between these similar sized species. It is noteworthy that the all-purpose territory of three male Superb Birds of Paradise, *Lophorina superba*, a species with only 24% fruit in its diet, averaged 1.5ha (range 1.2-1.7) (Beehler & Pruett-Jones, 1983). The availability of fruit in time and space may therefore have major effects on both male dispersion and home range.

Male Tooth-bills do not move far from their courts and, as would be expected, males at an exploded lek exhibit considerable overlap (mean = 50%) of home ranges. Those with closer courts show the greatest overlap, and males from different courts were observed to bathe in the same portions of creeks and to feed in the same trees. Although distances incurred in travelling to bathing and drinking locations, or those associated with leaf thefts, are likely to remain constant across years this will not be true of distances travelled to and from feeding locations. These latter distances will vary between years as different individual trees or species of tree fruit. Seasonal environmental differences, in particular fruit crop size, affect the length of Tooth-bill display seasons and the proportion of time that males attend courts (Moore, 1991; Frith & Frith,

1994). Fruit crop was poor during the 1989 display season (Moore, 1991). Consequently, males spent a greater proportion (36%) of their time absent from courts, to feed, during the 1989 season than during the 1980 season (21%) when fruit was abundant (Frith & Frith, 1994). During the exceptionally dry 1979 season an extremely poor fruit crop resulted in males spending even more time (48%) away from courts (Frith & Frith, 1994).

All the observed movements away from courts appeared to entail direct purposeful flights to food, water or leaf (court decoration) resources. Activities such as interactions with conspecifics or the collection of leaf decorations that were observed away from courts, during both foraging and non-foraging absences, were extremely brief (Table 5). Most absences were for foraging, representing 83% of total time absent with a mean duration of 18 mins (Table 5). Moore (1991) found that Tooth-bills tended to forage more in food trees closer to the court than those further away and as a result shorter foraging absences were more frequent than longer ones. Median distance travelled from courts exclusively for foraging at food trees was 32m (median range 27-119). Male 37 flew much further than the other three males to forage, often visiting fruiting trees some 380m to the east of his court that were not visited by the other males studied (Fig. 1). While males other than those of this study doubtless fed in these trees the observation suggests the possibility that males on an exploded lek may travel greater distances to utilise rich food resources where competition may be less. It is possible, however, that Male 37 also fed in this area due to the local accessibility of the creek (see Fig. 1).

Donaghey (1981) presented the only comparable data. He found that five rainforest-dwelling male Satin Bowerbirds, *Ptilonorhynchus violaceus*, mostly foraged for food within 50m of their bowers (83% of 83 foraging records) during the breeding season of October-December. He obtained almost identical results for four woodland-dwelling males (82% of 273 foraging records within 50m of bowers). His Satin Bowerbird's bowers did not form leks but were dispersed linearly along forest edges at a mean inter-bower distance of 312m (Donaghey, 1981).

Male Tooth-bills, like male Satin and other bowerbirds, must remain close to their court if they are to successfully display and attract females to mate (Frith & Frith, 1993) as do males of other, mostly lekking, passerines (Snow, 1962; Lill 1974a, b). Thus, irrespective of the size of a

meal eaten or the distance travelled to the food, males almost invariably return directly to their court in order to defend it from leaf stealing rivals and to call and display. In effect, male Tooth-bills attempt to maximise their time at their court (Moore, 1991). They can achieve this, however, only by utilising a food resource that is freely available and unable to be defended, namely, fleshy fruits. Snow (1976) considered a predominantly frugivorous diet one of the main pre-conditions to a mating system lacking pair bond and biparental brood care in which males spend much time attending and defending a traditional courtship area.

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REDISCOVERED PSEUDOSCORPION TYPE MATERIAL DESCRIBED BY BEIER FROM SOUTHEASTERN QUEENSLAND (ARACHNIDA: PSEUDOSCORPIONIDA)

MARK S. HARVEY

Harvey, M.S. 1994 12 01: Rediscovered pseudoscorpion type material described by Beier from southeastern Queensland (Arachnida: Pseudoscorpionida). *Memoirs of the Queensland Museum* 37(1):155-156. Brisbane. ISSN 0079-8835.

All or part of the type series of five pseudoscorpion species described by Beier (1969) from southeastern Queensland have been considered lost for some time. They have been recently found in the Department of Entomology, University of Queensland and transferred to the Queensland Museum. The specimens are documented. □ *Arachnida, Pseudoscorpionida, Tridenchthoniidae, Chthoniidae, type material.*

Mark S. Harvey, Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia; 15 December 1993.

Beier (1969) recorded several species of pseudoscorpions from southeastern Queensland, based upon material sent to him by Mr J.B. Williams. Five were new and a further two species were recorded from southeastern Queensland for the first time. Beier claimed to have returned most of the material to Mr Williams, then at Monash University, Melbourne, while retaining several specimens of two species in the collections of the Naturhistorisches Museum, Vienna. Despite efforts to trace these specimens, the material appeared to be lost (Harvey, 1981, 1985, 1989).

During a recent visit to the Department of Entomology, University of Queensland, Brisbane, I located the missing vials, and now take this opportunity to comment on the condition and status of the types.

All of the type material has been transferred to the Queensland Museum, Brisbane (QM).

Family TRIDENCHTHONIIDAE

Heterolophus australicus Beier, 1969

Heterolophus australicus Beier, 1969: 171-172, fig. 1.

MATERIAL EXAMINED

HOLOTYPE: ♀, Mt Tamborine, Joalah National Park, Queensland, 28°56'S, 153°12'E, berlesate, rainforest leaf litter, 16 Aug 1966, B. Cantrell, QMS21333.

PARATYPE: 1 tritonymph, same data as holotype, QMS21334.

REMARKS

The specimens are in fair condition, and the right chela is detached from the holotype. A recurrent typographical error by Beier (1969) referred to Mt Tamborine as "Mt Jamborine" and Joalah National Park as "Toalah National Park".

Anaulacodithella australica Beier, 1969

Anaulacodithella australica Beier, 1969: 172-174, fig. 2.

MATERIAL EXAMINED

HOLOTYPE: ♂ Lamington National Park, Queensland, 27°12'S, 153°10'E, extracted from leaf litter, 6 Mar 1965, B. Cantrell, QMS21335.

ALLOTYPE: ♀, Mt Glorious, Queensland, 27°20'S, 152°46'E, 11 Jul 1965, berlesate, rainforest leaf litter B. Cantrell, QMS21336.

PARATYPES: 1 ♂, 1 ♀, Landsborough, Queensland, 26°48'S, 152°58'E, Australia, leaf mould, mixed forest, 16 Jul 1965, F.A. Perkins, QMS21337; 8 specimens, Mt Clunie, east spur, Queensland, 28°20'S, 152°31'E, leaf mould, rainforest, 5 Apr 1953, T.E. Woodward, QMS21338; 16 specimens, Mt Tamborine, Joalah National Park, Queensland, 28°56'S, 152°12'E, berlesate, 16 Aug 1966, B. Cantrell, QMS21339.

REMARKS

The holotype and allotype are in fair condition, but the remaining specimens are extremely bleached and fragmented. The left chela of the holotype has been detached; the right chela of the allotype has been detached and subsequently lost.

Family CHTHONIIDAE

Morikawia queenslandica Beier, 1969

Morikawia queenslandica Beier, 1969: 174-175, fig. 3.

MATERIAL EXAMINED

SYNTYPES: 5 ♂, 3 ♀, Mt Tamborine, Joalah National Park, Queensland, 28°56'S, 153°12'E, berlese, rainforest leaf litter, 16 Aug 1966, B. Cantrell, QMS21341.

REMARKS

This species was transferred to the genus *Tyrannochthonius*, based on examination of the remaining syntypes lodged in Naturhistorisches Museum, Vienna (Harvey, 1989).

Morikawia semihorrida Beier, 1969

Morikawia semihorrida Beier, 1969: 176-177, fig. 4.

MATERIAL EXAMINED

HOLOTYPE: ♀, Mt Nebo, Queensland, 27°23'S, 152°47'E, rainforest leaf litter, 28 Mar 1967, J.B. Williams, QMS21340.

REMARKS

The recent transfer of this species to *Tyrannochthonius* (Harvey, 1989) based solely on the original description is confirmed by examination of the holotype. The right chela has been detached from the pedipalp.

Pseudotyrannochthonius queenslandicus
Beier, 1969

Pseudotyrannochthonius queenslandicus Beier, 1969: 177-178, fig. 5.

MATERIAL EXAMINED

HOLOTYPE: ♂, Mt Tamborine, Joalah National Park, Queensland, 28°56'S, 153°12'E, 16 Aug 1966, B. Cantrell, berlesc, QMS21342.
PARATYPE: 1 tritonymph?, same data as holotype, QMS21343.

REMARKS

The specimens are in fair condition.

Austrochthonius australis Hoff, 1951

REMARKS

Beier (1969) recorded this species from southeastern Queensland, based on one male from Mt Nebo, (berlesate, rainforest leaf litter, 28 Mar 1967, J.B. Williams), which is now lodged in the Department of Entomology, University of

Queensland. This specimen conforms to recent descriptions of the species (Kennedy, 1989).

Family OLPIIDAE

Xenolpium longiventer (L. Koch, 1885)

REMARKS

Beier (1969) recorded this species from southeastern Queensland based on a specimen from Mt Nebo (rainforest leaf litter, 28 Mar 1967, J.B. Williams), which is now lodged in the Department of Entomology, University of Queensland. The specimen is clearly not congeneric with the type of *X. longiventer* (BMNH), and in fact represents an undescribed species of *Protogarypinus*. Members of this genus are abundant in southeastern Australia, and many new species await description.

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SOME EARTHWORMS FROM THE WET TROPICS AND FROM BUNYA MOUNTAINS, QUEENSLAND (MEGASCOLECIDAE: OLIGOCHAETA)

B.G.M. JAMIESON

Jamieson, B.G.M. 1994 12 01: Some earthworms from the Wet Tropics and from Bunya Mountains, Queensland (Megascolecidae: Oligochaeta). *Memoirs of the Queensland Museum* 37(1): 157-180. Brisbane. ISSN 0079-8835.

A systematic study, supported by a cladistic analysis, indicates that North Queensland species of *Diporochaeta* warrant separate generic status, as *Terrisswalkerius* gen. nov. *Fletcherodrilus* gen. nov. represents an apomorphic clade of this assemblage which is, nevertheless, retained as a separate genus. The Bunya Mountains isolate of *Diporochaeta* merits separate generic status, as *Hiatidrilus bunya*, and *Cryptodrilus semicinctus*, from Grafton, on the Clarence River, New South Wales, is congeneric with it. The residue of *Diporochaeta* is a paraphyletic and polyphyletic entity requiring further resolution. The cladistic analysis also investigates wider relationships of the above genera with the remainder of the Perionychini. In the analysis the type-species of *Diporochaeta*, *D. intermedia*, is separated by other genera from those *Diporochaeta* species here assigned to *Terrisswalkerius* and, indeed, from all other included *Diporochaeta* species. The analysis suggests that *Perionychella*, currently subsumed in *Diporochaeta*, is the sister-taxon of the *Terrisswalkerius-Fletcherodrilus* assemblage. The phylogram is not inconsistent with the generic status of the remaining perionychin genera *Gratiophilus*, *Heteroporodrilus*, *Paraplutellus*, *Perionychella*, *Pinguidrilus*, *Plutellus*, *Pseudoperichaeta*, *Simsia*, and *Woodwardiella* but significant autapomorphies remain to be established for some of these. Within *Terrisswalkerius* the most plesiomorphic species appears to be *T. blounti*. *T. atavicus*, is the most derived species and forms the sister-taxon of *Fletcherodrilus*. Pairs of sister-species are: *T. grandis* and *T. terraereginae*, *T. millaamillae* and *T. mcdonaldi* sp. nov., *T. ather-tonensis* and *T. oculatus*, *T. kuranda* and *T. canaliculatus*, and *T. nashi* and *T. liber* sp. nov. A monophyletic, though weakly defined, species group contains *T. ather-tonensis*, *T. oculatus*, *T. canaliculatus*, *T. kuranda*, *T. crateris*, *T. nashi* and *T. liber*. The new species *T. covacevichae* and *Fletcherodrilus menurus* are also described. □ *Terrisswalkerius* gen. nov., *Hiatidrilus* gen. nov., *Fletcherodrilus*, *Diporochaeta*, *Perionychini*, cladistics.

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Diporochaeta was erected by Beddard (1890) with, as its type-species, the New Zealand species *Diporochaeta* (= *Perichaeta*) *intermedia* Beddard, 1889. Prior to the present work, *Diporochaeta* contained 78 Australian species. These species had been initially placed, on erection, in some eight genera in addition to *Diporochaeta*. Of these, five (*Cryptodrilus*, *Megascolex*, *Megascolides*, *Perionyx*, *Plutellus*) are still recognised as distinct genera, two (*Perionychella* and *Vesiculodrilus*) have been subsumed in *Diporochaeta* (see Jamieson, 1976b) and one (*Perichaeta*) in *Megascolex* (see Michaelsen, 1900). Here evidence will be presented, in a cladistic analysis, in support of removal on 'intuitive' grounds, of 16 species from North Queensland from *Diporochaeta* and their transfer to a new genus, *Terrisswalkerius*, and for transfer of two species to a further new genus, *Hiatidrilus*. The number of Australian species of *Diporochaeta* is thus reduced to 60.

Three new species are added to *Terrisswalkerius*. The status and phylogenetic affinities of *Fletcherodrilus* will also be investigated. Jamieson (1976b) observed that little other than the unpaired genital pores warranted separation of *Fletcherodrilus* from *Diporochaeta*, that inclusion in the latter genus as a subgenus would be sustainable, and that *Fletcherodrilus* may be regarded as the apomorph sister-group of *Diporochaeta*. A new species is added to *Fletcherodrilus*. Erection of a distinct genus for north Queensland species of *Diporochaeta* and the apomorphic status of *Fletcherodrilus* have been independently suggested by Dyne & Wallace (1994).

The status of the predominantly Western Australian genus *Gratiophilus* Jamieson, 1971b, was rendered uncertain by addition of North Queensland species to *Diporochaeta* by Jamieson (1976b) which blurred the distinction between the two genera. *Gratiophilus* was

retained by Jamieson (1974a) on the grounds, inter alia, that in Western Australian species the number of spermathecae was less (2 or 3 pairs) than the five pairs usual in *Diporochaeta* and that the avesiculate nephridia and totally lumbricin condition of the setae were constant whereas the combination of these characters was known in only one species of *Diporochaeta* from eastern Australia (Tasmania). It was concluded, however, that the low phenetic resemblance between *Diporochaeta* and *Gratiophilus* demonstrated by Wallace (1972) and the very distinct morphology of some *Gratiophilus* species suggested that this genus should be retained. The present study examines cladistic relationships of *Gratiophilus* to *Diporochaeta* s. lat. and includes in the analysis the type-species of all named genera of the Perionychini, viz. the 13 genera *Diporochaeta*, *Fletcherodrilus*, *Gratiophilus*, *Heteroporodrilus*, *Hiatidrilus*, *Paraplutellus*, *Perionychella*, *Pinguiculus*, *Plutellus*, *Pseudoperichaeta*, *Simsia*, *Terrisswalkerius*, and *Woodwardiella*.

Retention of *Perionychella*, for forms lacking nephridial bladders (and possibly with racemose prostates, as in the type-species) as a subgenus of *Diporochaeta* deserves consideration but was not upheld (Jamieson, 1976b) as the distinction between an avesiculate and a vesiculate group of species had become increasingly blurred. Thus Tasmanian *Diporochaeta mortoni* has avesiculate and, typically, vesiculate individuals (Jamieson, 1974a). *D. grandis* has vesiculate and avesiculate populations, or even segments in the same individual and in *D. terraereginae* (both are Queensland species) nephridial ducts are transitional between the two conditions. Perhaps more significantly, in an unpublished taxonomic (numerical) study vesiculate and avesiculate species formed mixed groups, especially where all nephridial characters are omitted. It is noteworthy that Michaelsen, who ignored the presence or absence of bladders, considered the avesiculate *D. atavia* to be merely a form of the vesiculate *D. athertonensis*, a decision indicating the closeness of the entities with the antithetic conditions, notwithstanding the view (Jamieson, 1976b) that they are distinct species.

Unless otherwise stated material studied is housed in the Queensland Museum (QM).

Terrisswalkerius gen. nov.

DIAGNOSIS

Setae numerous (>14) per segment. Genital markings other than porophores bearing the

female, male and spermathecal pores, absent. A pair of combined pores of vasa deferentia and tubular or tubuloracemose prostates on XVIII. Last hearts in XII or XIII. Gizzard in V or VI (or VII?) (well developed); intestinal caeca and typhlosole absent. Extramural calciferous glands absent. Nephridia stomate exonephric holonephridia with or without bladders; their pores in straight or sinuous lines but never with regular alternation. Spermathecae 1 to 5 pairs, rarely unpaired midventral, pre-testicular, diverticulate; diverticulum usually single, uniloculate; rarely double, rarely multiloculate.

DESCRIPTION

Terrestrial worms. Form circular in cross section or less commonly slightly depressed dorsoventrally; anus terminal. With or without pigmentation. Prostomium proepilobous to tanylobous. Body usually with a dorsal groove (canalicula) in part or the whole of its length. Dorsal pores present; in 3/4 - 6/7, usually 5/6. Setae perichaetine throughout. Nephridia in single lateral series throughout, or in irregularly sinuous series, varying from far dorsally to far ventrally but never showing regular alternation. Posterior limit of the clitellum shortly anterior to the male pores or including these. A pair of male pores on XVIII, each pore the combined opening of a prostate gland and the corresponding vasa deferentia. Female pores paired on XIV. Spermathecal pores 1 to 5 pairs, rarely unpaired midventral, between intersegmental furrows 4/5-8/9, rarely shortly behind the intersegments.

Dorsal blood vessel single, continuous onto the pharynx; last hearts in XII or, rarely, XIII; hearts in X posteriorly latero-oesophageal, each receiving a connective from the supra-oesophageal vessel and a lesser connective (sometimes absent?) from the dorsal vessel. Supra-oesophageal vessel restricted to the post-gizzard oesophagus, moderately to well developed. Subneural blood vessel absent. Gizzard in V or, more frequently, VI (or VII?) (well developed). Extramural calciferous glands not developed but oesophagus vascularized and often internally rugose in some segments from VIII to XVI. Intestine commencing in XVI to XIX, most frequently XVII; intestinal caeca and typhlosole absent. Nephridia simple, exonephric holonephridia throughout; tufted nephridia absent; bladders usually present, with or without diverticula; exceptionally (*D. grandis*, part.) avesiculate in the forebody and vesiculate in the hindbody. Holandric (testes in X and XI); seminal vesicles two to four pairs, in IX

to XII, exceptionally (*T. terraereginae*) in VIII (in addition to IX and XII), and often with pseudovesicles in XIII. Metagynous (ovaries and funnels in XIII). Prostates tubular or tubuloracemose, never racemose. Penial setae absent. Spermathecae diverticulate; diverticulum usually single, uniloculate; rarely double or multiloculate.

DISTRIBUTION

The Wet Tropics of eastern North Queensland, from the Paluma Range, 19S., near Townsville, north to the Upper Endeavour River shortly below 15°S.

TYPE SPECIES

Terrisswalkerius (= *Perichaeta*) *canaliculatus* (Fletcher, 1887a); here selected because its anatomy is well known and it is the most widely distributed species of the genus and therefore the most likely to be available for molecular and other studies.

ETYMOLOGY

Named in memory of Terry Walker. Gender masculine.

INCLUDED SPECIES

T. atavius (Michaelsen, 1916); *T. athertonensis* (Michaelsen, 1916); *T. barronensis* (Fletcher, 1886b); *T. blounti* (Jamieson, 1976b); *T. canaliculatus* (Fletcher, 1887a); *T. covacevichae* sp. nov.; *T. crateris* (Jamieson, 1976b); *T. erici* (Michaelsen, 1916); *T. grandis* (Spencer, 1900); *T. kuranda* (Jamieson, 1976b); *T. liber* sp. nov.; *T. mcdonaldi* sp. nov.; *T. millaamillaa* (Jamieson, 1976b); *T. montislewisi* (Jamieson, 1976b); *T. nashi* (Jamieson, 1976b); *T. oculatus* (Jamieson, 1976b); *T. phalacrus* (Michaelsen, 1916); *T. raveni* (Jamieson, 1976b); *T. terraereginae* (Fletcher, 1890).

KEY TO SPECIES OF TERRISSWALKERIUS

1. Spermathecal pores 5 pairs, in or shortly behind intersegmental furrows 4/5-8/9 2
- Spermathecal pores 1 to 4 pairs (rarely unpaired, midventral), in or shortly behind some or all of intersegmental furrows 5/6-8/9 4

Spermathecal pores 5 pairs

2. Spermathecal pores in a lines. Spermathecal duct very short. Last hearts in XIII *T. grandis*

Spermathecal pores median to a lines. Spermathecal duct long and slender though shorter than the ampulla. Last hearts in XII 3

3. Spermathecal pores of 8/9 c. 0.02 body circumference apart. Male pores c. 0.03 body circumference apart. Seminal vesicles in IX and XII. Nephridial bladders present *T. atavius*
- Spermathecal pores of 8/9 c. 0.06 body circumference apart. Male pores c. 0.1 body circumference apart. Seminal vesicles in XI and XII (or absent). Nephridial bladders absent *T. phalacrus*
4. Spermathecal pores in 4 intersegments, 5/6-8/9 or 4/5-7/8, paired or single 5
- Spermathecal pores 3 pairs or fewer 9

Spermathecal pores in 4 intersegments

5. Spermathecal pores in 5/6-8/9, unpaired, midventral *T. mcdonaldi* sp. nov.
- Spermathecal pores 4 pairs, in 4/5-7/8 or 5/6-8/9 6
6. Spermathecal pores 4 pairs, in 4/5-7/8 *T. terraereginae*
- Spermathecal pores 4 pairs, in 5/6-8/9 7
7. Male pores median to a lines, their papillae contiguous in the midline. Nephridial bladders absent *T. millaamillaa*
- Male pores between setal lines a and d, their papillae well separated in the midline. Nephridial bladders present 8
8. Prostomium tanylobous, with wide dorsal tongue. Nephropores in a straight series on each side *T. erici*
- Prostomium epilobous or proepilobous; with a deep middorsal groove which continues to the hind margin of the peristomium. Nephropores in an irregularly sinuous series, varying from far dorsally to far ventrally, on each side *T. kuranda*
9. Spermathecal pores 3 pairs, in 4/5-6/7 or in or shortly behind 6/7-8/9 10
- Spermathecal pores 1 or 2 pairs, in some of 5/6-8/9 16

Spermathecal pores 3 pairs

10. Spermathecal pores 3 pairs, in 4/5-6/7 11
- Spermathecal pores 3 pairs, in or shortly behind 6/7-8/9 13
11. Spermathecal diverticulum long and tortuous. Spermathecal pores in the vicinity of d to e lines 12
- Spermathecal diverticulum short and clavate. Spermathecal pores between a and b lines *T. montislewisi* (part.)

12. Spermathecal diverticulum longer than ampulla plus duct. (Spermathecal pores in *d* lines) . . .
 *T. barronensis*
 Spermathecal diverticulum shorter than ampulla plus duct. (Spermathecal pores in *d-e* lines) . . .
 *T. raveni*
13. Male pores very close together, almost contiguous midventrally, on a common papilla . . .
 *T. athertonensis*
 Male pores well separated, between setal lines *b* and *f*, on a pair of papillae 14
14. Spermathecal diverticulum simple, shortly clavate 15
 Spermathecal diverticulum composite, consisting of as many as 4 parallel conjoined tubes with terminal, knoblike seminal chambers; approximately as long as the spermathec
 *T. oculatus*
15. Spermathecal pores varying from setal lines 3 to 5. Male pores between setal lines 4 to 7. Prostate glands restricted to XVIII . . . *T. canaliculatus*
 Spermathecal pores in *b* lines. Male pores in *ab*. Prostate glands concealing the gut, in XVIII-XXI *T. covacevichae* sp. nov.

Spermathecal pores 2 pairs

16. Spermathecal pores 2 pairs, in 5/6 and 6/7 . . .
 *T. montislewisi* (part)
 Spermathecal pores 1 pair, in 6/7 or 7/8 or 8/9 17

Spermathecal pores 1 pair

17. Spermathecal pores 1 pair, in 8/9. Spermathecal diverticulum long and tortuous 18
 Spermathecal pores 1 pair, in 6/7 or 7/8 19
18. Spermathecal pores in setal lines *c* to *d*.
 *T. nashi*
 Spermathecal pores well median of setal lines *a*
 *T. liber* sp. nov.
19. Spermathecal pores 1 pair in 6/7 *T. crateris*
 Spermathecal pores in 7/8 *T. blounti*

Terrisswalkerius athertonensis (Michaelsen, 1916) comb. nov. (Figs 1; 2A,B)

- Perionyx* (*Diporochaeta*) *athertonensis* Michaelsen, 1916: 7-9, pl.1, fig.7.
Diporochaeta athertonensis; Jamieson, 1971c: 83; Jamieson, 1976b: 14, figs 1, 9a, table 1.
Perionychella (*Perionychella*) *athertonensis*; Jamieson, 1974a: 221.

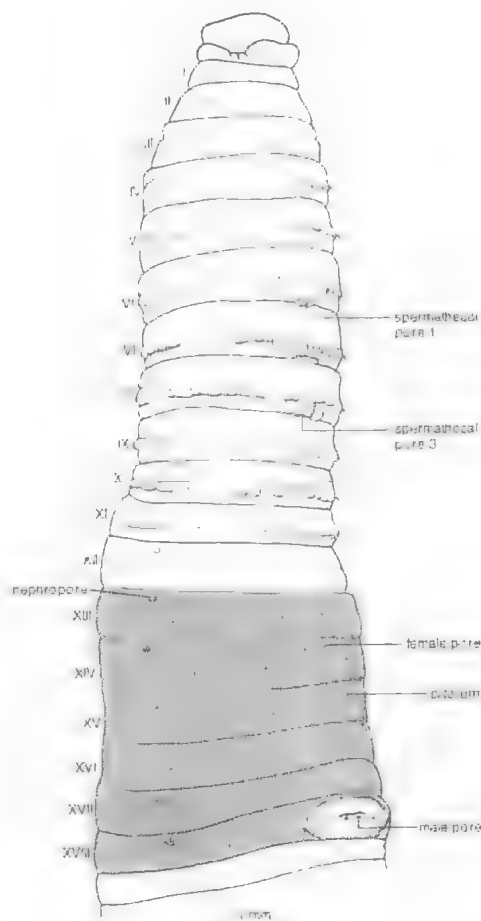


FIG. 1. *Terrisswalkerius athertonensis* (Michaelsen, 1916), Mt Lewis, QMG9210. Forebody and clitellar region, lateroventral view.

TYPE LOCALITY

17°16'S.145°29'E., Atherton. 15°39'-27°52'S.145°15'E.-15312'E., Cedar Creek. All Queensland.

MATERIAL EXAMINED

SYNTYPES: Zoology Museum Hamburg HMV8481 (re-examined), HMV8482 (now represented by soil debris only). Stockholm Museum NHRS1245.

NEW RECORD: 16°34'S. 145°17'E., Mt Lewis, in rainforest, F. Little and Queensland Museum Party, 7 Nov 1975, a single, previously dissected, clitellate specimen, QMG9210. (This material was correctly identified by R. Raven as *Diporochaeta athertonensis*, the first sighting since Michaelsen's 1916 description); 2 clitellate specimens, rainforest, 6kms from Malanda Falls Environmental Park, on road to Atherton, B.G.M.

Jamieson, 12. Dec 1994, QMG211454. All in Queensland.

DESCRIPTION

(The following account combines descriptions of all known material. The single specimen from Mt Lewis is a posterior amputee).

Length 36–68 mm, width 3–5 mm, segments 98–108. Pigmented violet brown, little colour remaining in Mt Lewis specimen. Tanylobous. Body canaliculate throughout. First dorsal pore 5/6. Setal circle regularly interrupted ventrally, dorsally irregularly; *a* lines regular throughout; *b* lines regular throughout or for much of body length; *c* lines less regular; in mid- and hind-body, *aa* = 1.5–2 *ab*; *dd* 1.3–2.3 *yz*, in anterior segments much larger. Intersetal spacing dorsally irregular and in general wider than ventrally, except in forebody. Setal numbers (Michaelsen): 10/VII, 15/V, 22/VIII, 24/X, 36/XIX, 35/XXVI, 36/LXX, 38/LXXI; 23 in XII, 40 in LXXVI (Mt Lewis). Nephropores (see also internal description) visible as a straight series on each side, immediately ventral of setal lines 10 on clitellum. Clitellum annular, XIII–1/2XVIII, XVIII; intersegmental furrows, setae, nephridial and dorsal pores clearly visible or (Mt Lewis) dorsal pores occluded. Male pores scarcely visible, very near ventral midline, 0.11–0.2 mm apart (Mt Lewis) in a transversely oval midventral glandular field. Female pores (Mt Lewis) a pair of minute points, shortly median of setae *a*, nearer anterior border than they are to setal arc of XIV. Spermathecal pores, hardly externally recognizable, 3 pairs, in 6/7–8/9, very near ventral midline, 0.05–0.07 mm apart, or (Mt Lewis) 0.08 mm and about one half *aa* apart. Genital markings absent.

Septa from 6/7 well developed, 6/7–8/9 thin, 9/10–12/13 slightly thickened, the remainder thin (type material). Dorsal blood vessel single; last hearts in XII; large and latero-oesophageal in X–XII. Gizzard large, in VI or (Mt Lewis) apparently V. Oesophagus in XII–XIV with folded, vascularized walls or (Mt Lewis) X–XVI vascularized; but lacking extramural calciferous glands and with no development of large paired blood vessels. Intestine commencing abruptly in XVI or (Mt Lewis) XVII; typhlosole and caeca absent. Nephridial bladders (not mentioned by Michaelsen), in the syntypes, wide tubes, those in II convoluted and discharging in *z* lines, succeeding bladders progressively more ventral so that by V they are in setal lines 7. Nephropores in 9 on XII, 8 on clitellum and 12 caudally. By V vesicles take form of a tube with an abrupt lateral bend at

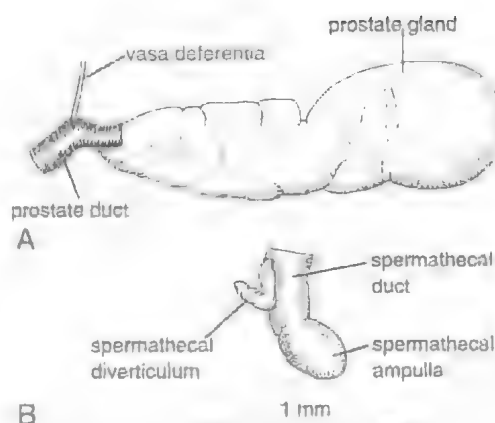


FIG. 2. *Terrisswalkerius athertonensis* (Michaelsen, 1916). Mt Lewis, QMG9210. A, right prostate; B, right posterior spermatheca.

c. midlength, two limbs parallel, ectal limb wide and often bent near pore (V-shaped bladders). In anterior intestinal region ental limb has become so narrow that it can scarcely be considered part of bladder and is so closely adherent to ectal limb that bend has spurious appearance of a diverticulum. This form persists to caudal extremity and although ental limb widens slightly it remains much narrower than ectal limb. In Mt Lewis specimen nephridial postseptal portions commence in II and a large preseptal funnel is demonstrable for those of III and less certainly II; ducts of the first three pairs are dilated but questionably to be considered bladders; thereafter they form definite bladders; those of V are V-shaped and those of anterior intestinal region similarly conform with syntypes. Two pairs of iridescent sperm funnels in X and XI; racemose seminal vesicles in IX and XII (Mt Lewis). Prostates tubular, almost confined to XVIII (syntypes and Mt Lewis); central lumen (Michaelsen) simple, about one eighth width of gland; wall of gland with two layers of glandular cells overlain by peritoneum, cells of inner layer in groups around apparently lumenless axes. Duct (all specimens) well defined from gland; about one fourth as long, much thinner and muscular. The two vasa deferentia of a side running close together and joining prostate duct at its midlength before (Michaelsen) passing distally to fuse with its lumen shortly before distal end. Penial setae absent. Ovaries wide and bushy, oviducal funnels large; oviducts short and straight. Spermathecae 3 pairs; ampulla smooth, saclike or ovoid, ducts sharply demarcated, two thirds width of ampulla

and somewhat shorter or (Mt Lewis) approximately as long; a slender clavate to digitiform diverticulum, with simple lumen, entering duct in body wall or (Mt Lewis) near its base and shorter than ampulla plus duct.

REMARKS

The new material, from Mt Lewis, agrees closely with the type material in most respects, indicating conspecificity. The difference of one segment recorded in the position of the gizzard and intestinal origin between the type and Mt Lewis material is not, however, usual intraspecifically and requires confirmation from better preserved material if available.

Terrisswalkerius covacevichae sp. nov. (Figs 3; 4A,B)

TYPE LOCALITY

17°33'S.145°34'E., Mt Fisher, N.E. Queensland, J. Covacevich, V.E. Davies, R. Raven, 23.iv. 1978.

MATERIAL EXAMINED

HOLOTYPE: QMG211447 ex QMGH1991.

PARATYPE: QMG211448 ex QMGH1991.

DESCRIPTION

Length (holotype, H, is a posterior amputee), 125mm (paratype, P), width 5.0mm (P), 6.2mm (H); segments 222 (P). Body not depressed, Pigmentless, excepting pale brownish grey clitellum, in alcohol. Prostomium tanylobous; its anterior half, and ventral surface bisected but body only weakly canaliculate; peristomium short. First dorsal pore 5/6 (P), 6/7 (H). Setae 28 in XII, 47 caudally; *aa* and, mostly, *zz* conspicuous breaks; *a* lines regular, *z* lines irregular, in hindbody and with some irregularity in first few segments; in XII, *aa:ab:bc:cd:yz:zz* = 2.2:1.0:1.2:1.0:1.0:6.6; setae *a* and *b* absent from XVIII. Nephropores clearly visible a short distance behind clitellum near anterior borders of their segments, laterally situated, in straight longitudinal lines in setal lines 11 or near this; not observed (though present) in forebody. Clitellum annular, XIV-XVII but dorsolaterally from anterior 1/3XIII; dorsal pores occluded in 14/15 to 16/17 where these intersegments are weaker. Male pores a pair of minute pores, in *ab*, each with a whitish rim, on large porophores which expand XVIII anteriorly and posteriorly and are somewhat medianly inclined so that male pores seem to be near their median borders; *a* deep depression

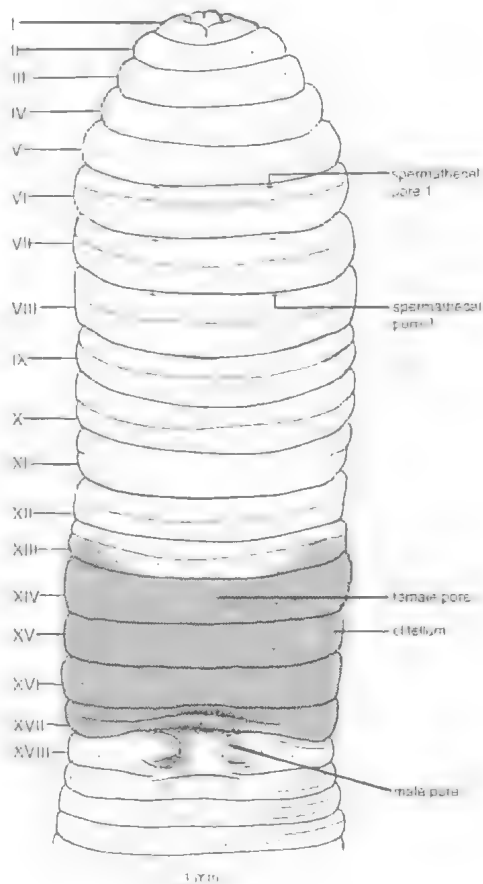


FIG. 3. *Terrisswalkerius covacevichae* sp. nov., holotype, QMG211447. Forebody and clitellar region, ventral view.

present between porophores and behind setal arc of XVII. Accessory genital markings absent (H, P). Female pores small transverse slits immediately anteromedian to setae *a* of XIV (P). Spermathecal pores 3 pairs of simple transverse slits at anterior borders of VI, VII and VIII, in *b* lines, sometimes hidden in anterior intersegmental furrow (H, P).

Thickest septa 10/11-12/13, strongly thickened. Dorsal blood vessel single, continuous onto pharynx. Last hearts in XII; those in X-XII large and arising from supra-oesophageal without recognizable connection to dorsal vessel; those in VII-IX slender, and dorsoventral only. Gizzard large, barrel-shaped with anterior rim, and strongly muscular, in VI; septa 6/7 and 7/8

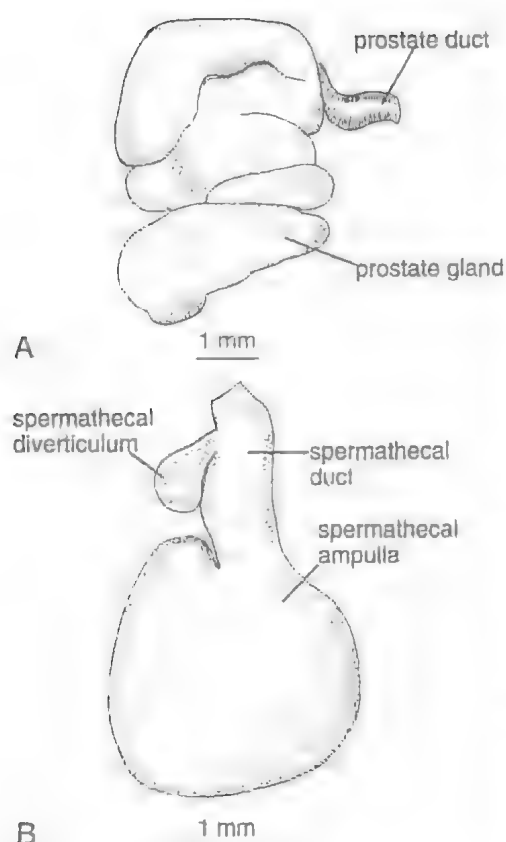


FIG. 4. *Terrisswalkerius covacevichae* sp. nov., holotype, QMG211447. A, Right prostate, ventral view; B, right anterior spermatheca, ventral view.

diaphanous and applied to its posterior surface; gizzard deflecting septa posteriorly so that its posterior end is invested by a pair of long, anteriorly projecting lobes of seminal vesicles of IX. Oesophagus with circumferential vascular striae in IX–XVI, virtually obliterated by gizzard in VII and VIII; greatly expanded in XV and XVI where it attains the width of the intestine; dilatation not constricted off from oesophageal lumen but slightly depressed middorsally, giving a suggestion of a paired condition and internally with circularly arranged, moderate vascular rugae. Oesophagus narrow and whitish in XVII and XVIII. Intestinal origin XIX, although bulging forward so as to appear to commence in XVIII; typhlosome and caeca absent (H, P). Intestinal contents a fine reddish 'silt', of unknown composition, and vegetable matter (including, in H, a recurved thorn filling much of lumen). Nephridia stomate, vesiculate holonephridia; in anterior

region of forebody duct is bent on itself and distal limb is dilated as an elongate bladder which extends at bend as a very short diverticulum; in intestinal region duct joins bladder near its equator and an elongate diverticulum extends laterally from bladder; egress of bladders at body wall is more lateral in intestinal region than further anteriorly (H, P). Holandric; testes (?) and fairly small scarcely iridescent funnels in X and XI; large racemose seminal vesicles with several large loculi which are themselves further subdivided, in IX and XII (H, P); those in IX with a median wing-like or tongue-like portion which extends onto gizzard (H) or this extension not evident, although investing gizzard (P). Ovaies, each a large plate of oocytes, and small funnel, in XIII. Prostates with massive glands enwrapping and concealing alimentary canal, in XVIII–XXI; deeply incised by septa but otherwise smooth surfaced and not notably subdivided. Spermathecae 3 pairs, each with a large, ovoid ampulla and a well developed only slightly shorter duct; duct bears, at its ectal fourth, a subspheroidal, almost sessile, inseminated diverticulum. By internal septation there are no spermathecae in VIII, segment anterior to that containing anterior seminal vesicles, last pair of spermathecae being in VII. However, external examination confirms the posterior pair of spermathecal pores anteriorly in VIII. The internal septation is therefore anomalous, disagreeing with external segmentation (H, P).

ETYMOLOGY

Named for Ms Jeanette Covacevich.

REMARKS

Although in the key *T. covacevichae* forms a couplet with *T. canaliculatus*, the latter differs substantially in the following features: $\alpha\alpha$ is wider, nephropore rows are irregular, male and spermathecal pores are more lateral, intestinal origin is more anterior (XVII), nephridial bladders are adiverticulate, and seminal vesicles are in XI and XII.

Terrisswalkerius mcdonaldi sp. nov. (Figs 5; 6A,B)

TYPE LOCALITY

17°38'S. 145°32'E., Majors Mtn. N.E. Queensland, coll. J. Covacevich, K.R. McDonald and R. Raven, 14–19.iv. 1978.

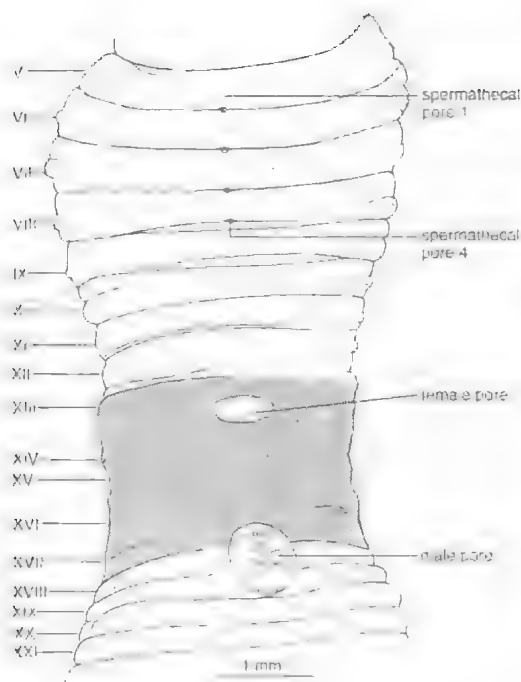


FIG. 5. *Terrisswalkerius mcdonaldi* sp. nov., holotype, QMG211450. Region of male and spermathecal pores, ventral view.

MATERIAL EXAMINED

HOLOTYPE: QMG211450 ex QMGH1994

DESCRIPTION

Length 31mm, width (midclitellar) 2.4mm, segments 106. Body not depressed. A faint trace of purplish pigmentation dorsally in alcohol. Prostomium tanylobous (?); body not canaliculate. First dorsal pore 4/5. Setae 36 in XII; 36 caudally; ventral and dorsal interruptions small but visible throughout in XII $aa:ab:bc:cd:yz:zz = 1.8:1.0:1.0:0.7:1.1:1.8$. Nephropores not externally recognizable. Clitellum annular, yellow brown, 1/2 XIII-XVII; intersegmental furrows obliterated; dorsal pores occluded. Male pores a pair in setal arc of XVIII, on very small papillae separated medianly by a minute papilla, situated in an elongate oval area which extends from setal arc of XVII to posterior XIX and has a tumid rim surrounding a depressed and apparently glandular area anterior and posterior to male papillae. Female pores paired (?) in a transverse slit shortly anterior to setal arc of XIV, in a transversely oval slightly tumid field. Spermathecal pores 4, un-

paired, midventral, in 5/6-8/9, not recognisable unless intersegmental furrows are held open.

Dorsal blood vessel single. Last hearts in XII. Gizzard large, firmly muscular, in VI (?), with conspicuous anterior rim; preceded by a large, but not dilated, soft-walled proventriculus. Oesophagus with a pair of circumferential blood vessels, and dilated, in XIV, XV and XVI, with many discrete internal vascular folds; these dilations not constricted off from oesophageal lumen, but probably to be considered true calciferous glands; oesophagus in XVII short and narrow and invaginated into posterior face of calciferous glands of XVI. Intestinal origin XVIII; typhlosole absent; contents finely particulate vegetable matter. Nephridia stomate, avascular holonephridia; each discharging at body wall through a long duct which, although lacking a bladder, has a clearly visible lumen; egress of ducts is in vicinity of setal rows 10 and 11 in forebody and in anterior intestinal region, the row on each side not notably irregular. Holandric; large, iridescent free funnels in X and XI; seminal vesicles small but elongate in XI, very small in XII, not subdivided into loculi. Ovaries, with several delicate strings of oocytes, which are terminally large, in XIII; ovisacs not recognizable. Prostates tubuloracemose, externally thickly tubular and almost smooth walled with some minute surface papillation, restricted to XVIII in which they extend laterally from their ducts; the distal third recurved on remainder of gland; each muscular duct describing a posterolateral loop; conjoined vasa deferentia of its side joining duct at about one seventh of its length from gland. Penial setae absent. Four unpaired spermathecae present, each with a tortuous

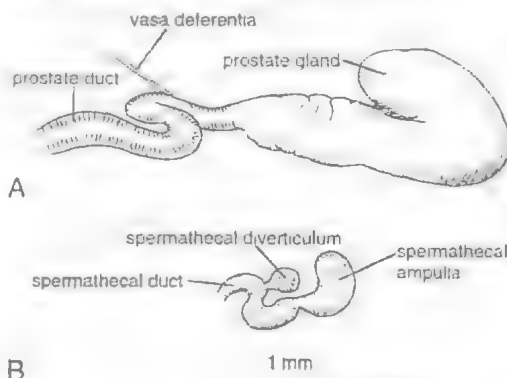


FIG. 6. *Terrisswalkerius mcdonaldi* sp. nov., holotype, QMG211450. A, right prostate; B, right spermatheca of VIII.

digitiform or narrowly saccular ampulla, continuous with and not demarcated from its duct; a subspheroidal diverticulum almost sessile on spermatheca at a point which arbitrarily may be considered the ental end of duct.

ETYMOLOGY

For Keith R. McDonald.

REMARKS

Terrisswalkerius mcdonaldi appears closest morphologically and, presumably phylogenetically, to *T. (=Diporochaeta) millaamillaa* (Jamieson, 1976b), from nearby Millaa Millaa. *T. millaamillaa* is also a very small species resembling *D. mcdonaldi* in location of the first dorsal pore in 4/5; nephropores in straight or nearly straight rows; clitellum on XIV-XVII; male pores median to *a* lines in an oval field; absence of accessory genital markings (as in all *Terrisswalkerius*); spermathecal pores in 4 intersegments, 5/6-8/9; last hearts in XII; prostates restricted to XVIII, recurved entally, and spermathecae elongate sacciform, with poorly demarcated duct and clavate, almost sessile diverticulum. It differs from *T. millaamillaa* in the unpaired condition of the spermathecal pores which is unknown elsewhere in *Terrisswalkerius* although invariable for *Fletcherodrilus*. Dilatation and internal folding of the oesophagus in *T. millaamillaa* (in XV and XVI) is less developed than in *T. mcdonaldi*.

Terrisswalkerius liber sp. nov. (Figs 7; 8A,B)

TYPE LOCALITY

15°45'S. 145°17'E., Home Rule, near Slaty Ck, N.E. Queensland, Under fallen staghorn fern, Queensland Museum party, 25.x.1974.

MATERIAL EXAMINED

HOLOTYPE: QMG211445 ex QMG9010.
PARATYPE: QMG21446 ex QMG9010.

DESCRIPTION

Length (holotype, H, is posterior amputee) 170 mm (previously dissected paratype, P), width 7 mm, segments 150. Body not depressed. Purplish grey dorsally; intersegmental furrows and ventral surface pale flesh coloured, in alcohol. Prostomium prolobous (H) or very slightly indenting peristomium (P), with open lateral margins extending to half peristomium; deeply canaliculate dorsally and bisected ventrally; body canalicu-

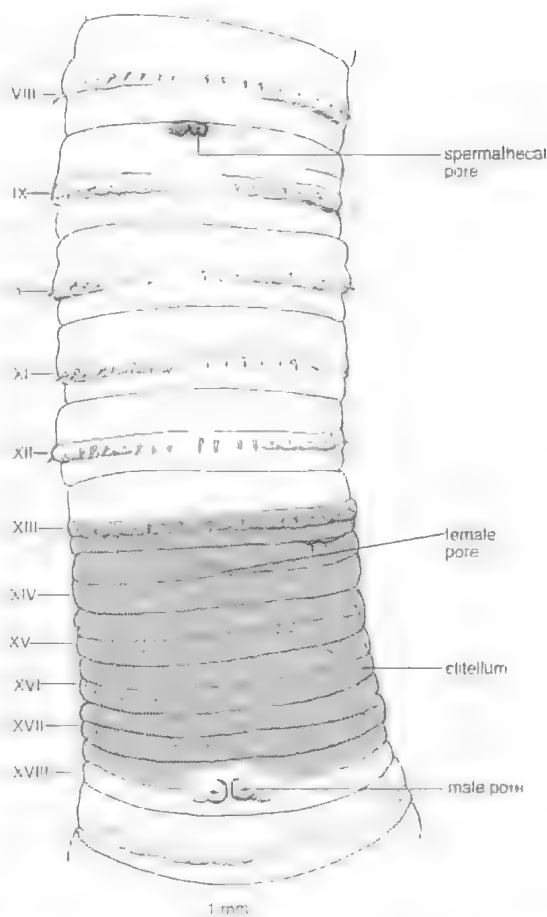


FIG. 7. *Terrisswalkerius liber* sp. nov., holotype, QMG211445. Region of male and spermathecal pores, ventral view.

late. First dorsal pore 5/6 (H, P). Setae 24 in XII; $aa:ab:bc:cd:yz:zz = 2.3:1.0:1.3:1.4:1.9:25.5$; ventral break narrow in forebody but moderately wide in hindbody; dorsal break extremely wide throughout forebody, so that setae are visible only laterally; narrower but very irregular posteriorly; several of the more dorsal rows not visible on clitellum but visible before and behind it; setae in forebody very strongly protruding in a posterior direction. Nephropores, each with a dark encircling field, conspicuous in an almost straight line on each side on clitellum, almost exactly lateral, in setal lines 11 relative to XIII. Clitellum annular, not strongly developed; pale reddish brown; from setal annulus of XIII to presetal annulus of XVIII, inclusive; intersegmental furrows weaker and not paler; dorsal pores retained; canalicula weaker. Male pores cruciform slits, in

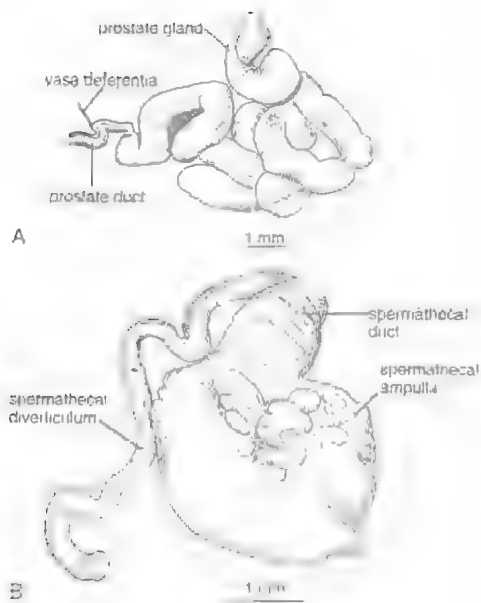


FIG. 8. *Terrisswalkerius liber* sp. nov., paratype. QMG211446. A, right prostate; B, left spermatheca, dorsal view.

setal arc of XVIII, in *a* lines, on a pair of small rounded papillae which are poorly defined laterally and fill middle third of segment and are almost in contact midventrally (H, P). Accessory genital markings absent. Female pores immediately anteromedian to setae *a*, on a low whitish presetal elevation in XIV (H, P). Spermathecal pores 1 pair, shortly posterior to intersegmental furrow 8/9, each a clearly visible minute pore on a very small but well defined wart-like papilla in a common sharply defined depression.

Septa 10/11–12/13 greatly thickened (H). Dorsal blood vessel single; dorsoventral commissurals in V–XII; those in X–XII large, heart-like and latero-oesophageal, originating by a large branch from the supra-oesophageal vessel and a thin, scarcely recognizable branch from the dorsal vessel (H, P). Gizzard very large, elongate and firmly muscular, in V, ensheathed by the extremely thin septa 5/6 and 6/7; its posterior end at level of VIII relative to external segmentation; obliterating oesophagus in VI and VII (H, P); a large muscular proventriculus in IV giving an almost digiceriate appearance (H). Oesophagus segmentally dilated and vascular, with a circumferential blood vessel on each side, in XIII–XVI; but dilatations not cut off from gut. Intestinal

origin 1/2XVII (H, P). Nephridia stomate, vesiculate holonephridia with large pyriform bladders; slender duct joining bladder slightly subterminally in pharyngeal region and increasingly ectal of apex of bladder posteriorly but recognition of a diverticulum unwarranted, Holandric; very large iridescent seminal funnels in X and XI; seminal vesicles a pair of large simple almost smooth-surfaced sacs on posterior septum of IX (H, but not P); and anterior septa of XII and, remarkably, XIII (H, P). Ovaries moderate sized laminae of many oocytes ventral to putative seminal vesicles of XIII (H, P). A pair of small sacs on anterior face of XIV may be ovisacs. Prostates slender, tubular and much coiled, in XVIII and XIX (P), or extending into XXI (H); slender muscular sinuous ducts discharging near midventral in XVIII, each receiving parallel vasa deferentia of its side at midlength (H, P). Spermathecae a single pair, each with a very large saccular ampulla with, in its ectal half, a papillated surface, a well demarcated annulated duct; and a terminal, tubular, sinuous, inseminated diverticulum which is longer than combined ampulla and duct (H, P).

ETYMOLOGY

From the Latin *liber* = free, reflecting the name of the type-locality.

REMARKS

Terrisswalkerius liber is very similar morphologically to *T. nashi* (Jamieson, 1976b; see below) and is undoubtedly its sister-taxon. Of the few species of the genus with a single pair of spermathecal pores, *T. liber* and *T. nashi* are the only ones in which they are at intersegment 8/9. *T. liber* differs in the close apposition of the spermathecal and male pores which are significantly wider apart in *T. nashi*. Sympatry of *T. nashi* and *T. liber* at Home Rule strengthens rather than weakens the grounds for separating the two entities and the difference in separation of the genital pores suggests that interbreeding would not occur between the two forms. Nevertheless, reproductive isolation remains to be established.

Terrisswalkerius nashi
(Jamieson, 1976b) comb. nov.

Diporochaeta nashi Jamieson, 1976b: 41–42, figs 1, 11b, 14j, 15m, 16n–p, table 2.

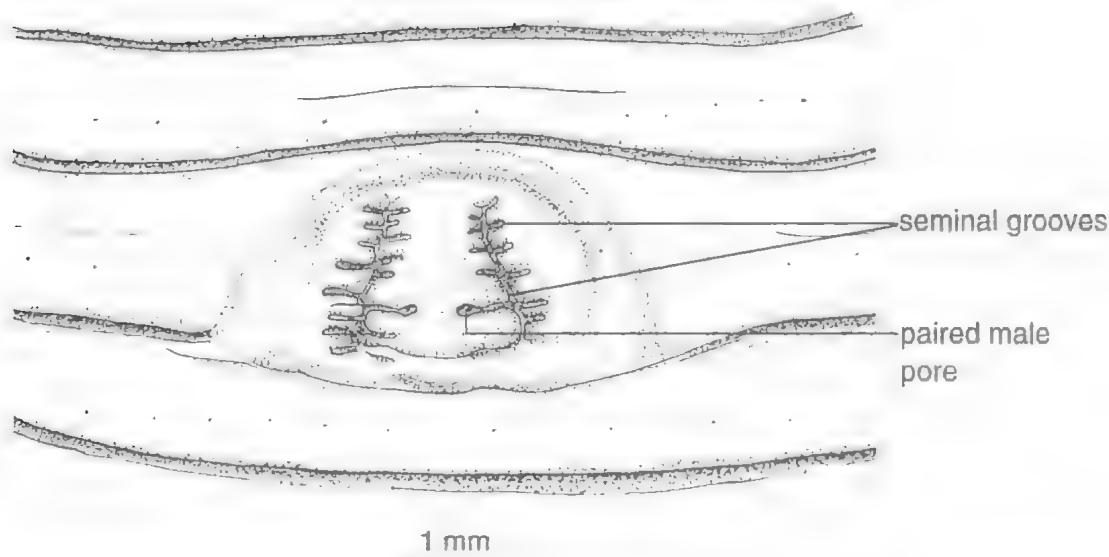


FIG. 9. *Fletcherodrilus menurus* sp. nov., holotype, QMG211435. Lyrate condition of seminal grooves and two putative male pores when male field is extruded.

TYPE LOCALITY

16°34'S.145°17'E., Mt Lewis, rainforest.
16°05'S.145°28'E., Cape Tribulation, rainforest.
15°55'S.145°21'E., Bloomfield River Mission,
S. of Cooktown. All Queensland.

MATERIAL EXAMINED

HOLOTYPE: QMG8357, Mt Lewis.

PARATYPES: QMG8358; 7 specimens, QMG8359-8364; Leiden Museum (LM)15242; 9 specimens, LM15243-15251; LM15252; QMG98373.

NEW RECORDS: QMG8987, 15°46'S. 145°20'E., Mt Hartley, via Home Rule, C. Tanner, J. Covacevich, V. Davies & T. Tebble, 1 specimen; QMG8988, 15°45'S. 145°17'E., Home Rule, under log, near Slaty Ck, granite track, closed forest, K. McDonald, D. Joffe & J. Covacevich, 11. xi. 1974, 1 specimen in two pieces. QMG8989, Home Rule, on track near falls, T. Tebble, 23. x. 1974, 1 specimen; QMG9158, Twelve Mile Scrub, Gap Creek, under rock, V. Davies 28. xi. 1975; QMG9209, 16°34'S. 145°17'E., Mt Lewis, dense moist rainforest with palms, under and in logs, R. Raven, 7 Nov. 1975; QMG10294, 15°42'S. 145°13'E., Helenvale, 12m scrub, in rainforest, P. Filewood, 24.vii.1976.

REMARKS

Specimens with a single pair of spermathecal pores, in intersegmental furrow 8/9 (a feature restricted in *Terrisswalkerius* to *T. nashi* and *T. liber*), and with these pores and the male pores

well separated, being in the vicinity of setal lines *bc* to *cd* or *d*, represent new records of *T. nashi*. All have the extremely wide dorsal interruption of the setal rings in the forebody, so that almost the entire dorsal surface lacks setae, a condition seen also in *T. liber*. A previously dissected specimen from Twelve Mile Scrub confirms presence of a long tortuous spermathecal diverticulum (the diverticulum of the left spermatheca passing under the ventral nerve cord, in this specimen, as occurs in *Fletcherodrilus*); sperm funnels in X and XI; seminal vesicles in XII and XIII, as also in the new Mt Lewis material (though the additional pair in IX, in the type-description, are not present); last hearts in XII; conspicuous pyriform nephridial bladders; and ovaries in XIII below the putative seminal vesicles. All of these internal features are also seen in *T. liber*. Dorsal mamillations of the spermathecal ampullae, as in *T. liber*, are seen in the specimen from Twelve Mile Scrub but not in that from Mt Lewis.

Fletcherodrilus Michaelsen, 1891 emend.

DIAGNOSIS

Unpaired male and prostatic pores; calciferous glands in XIII-XV; intestinal origin in XVIII; thickly tubular (tubuloracemose?) prostates;

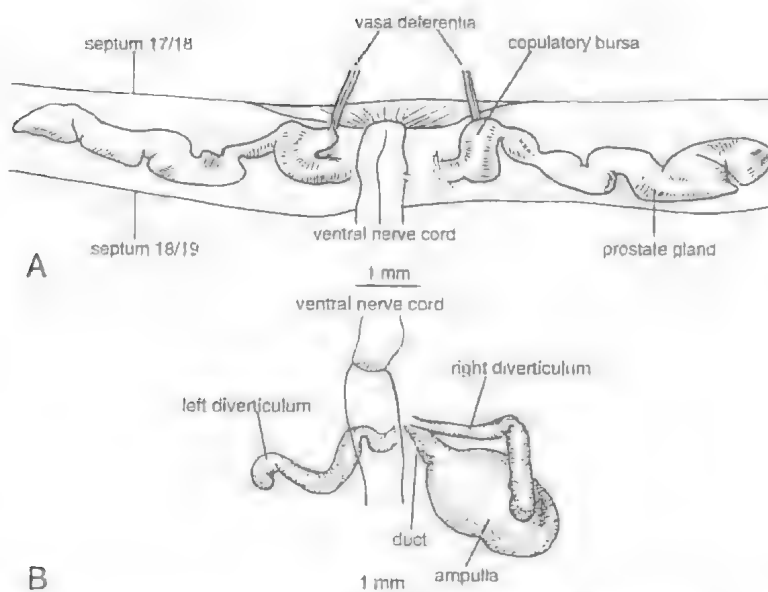


FIG. 10. *Fletcherodrilus menurus* sp. nov., holotype, QMG211435. A, dorsal dissection to show prostate glands; B, spermatheca of IX.

junction of vasa deferentia with the prostate ducts well ectal of the glands; spermathecae with irregularly ovoid ampullae and digitiform diverticula at the body wall.

DESCRIPTION

Medium to large terrestrial worms (85–325 mm) with < c. 200 segments. With strong purplish to brown parietal pigmentation. Prostomium slightly epilobous to epitanylobous. Body dorsally canaliculate. First dorsal pore 4/5 or 5/6. Setae 8 to numerous in setigerous segments; if 8, setae *c* and *d* distant, not paired. Penial setae absent. Nephropores in *d* lines or (*sigillatus*) in a sinuous line. Clitellum annular, occupying 4 to 5 1/2 segments, beginning in XIII or XIV. The combined opening of the male and prostatic pore unpaired, midventral. Accessory genital markings present (midventral plications in the vicinity of the spermathecal pores) or absent. Female pores anteromedian to setae *a* of XIV, inconspicuous. Three or 5 unpaired, midventral spermathecal pores, ending at 8/9.

Some preclitellar septa thickened. Gizzard well developed, in VI or VII. Calciferous glands lateral, sessile pouches in XIII and XIV or XIII, XIV and XV, with internal laminae but not constricted off from the oesophagus. Intestine commencing in XVIII; typhlosole and caeca absent. Dorsal blood vessel continuous onto the pharynx. Last hearts in XII; those in X–XII latero-

oesophageal. Supraoesophageal vessel in IX (and further forward?) to XII and XIII. Subneural vessel absent. Nephridia stomate, vesiculate holonephridia; postseptal bodies commencing in II; bladders with or without lateral diverticula. Testes and funnels free, in X and XI; seminal vesicles 4 pairs, in IX–XII, or 2 pairs in XI and XII, with or without pseudovesicles in X. Ovaries and funnels in XIII; ovisacs absent. Prostates thickly tubular (tubuloracemose?); vasa deferentia joining the muscular prostate ducts ectal to the glands to as far as the midlength of each duct; the ducts sometimes at least

discharging through a midventral bursa. Spermathecae unpaired, each discharging anteriorly in its segment; duct shorter than the ampulla and bearing ectally 1 or 2 digitiform diverticula.

DISTRIBUTION

Widespread from the Richmond River, New South Wales, to Cape York Peninsula, Queensland.

TYPE SPECIES

Cryptodrilus (?) *unicus* Fletcher, 1889.

INCLUDED SPECIES

F. affinis (Stephenson, 1933); *F. fasciatus* (Fletcher, 1890); *F. menurus* sp. nov.; *F. sigillatus* (Michaelsen, 1916); *F. unicus* (Fletcher, 1889).

KEY TO SPECIES OF *FLETCHERODRILUS*

1. Setae 8 per segment 2
Setae > 8 per segment 4
2. Spermathecae each with a single diverticulum *F. affinis*
Spermathecae each with two diverticula 3
3. Body uniformly pigmented though paler ventrally. Gizzard in segment VI. Calciferous glands 3 pairs, in XIII, XIV and XV. Seminal vesicles 2 pairs, in X and XI *F. unicus*
Body with transverse pigmented stripes. Gizzard in segment VII. Calciferous glands 2 pairs, in

TABLE 1. *Fletcherodrilus menurus*. Setal ratios in segment XII.

| | aa | ab | bc | cd | yz | zz |
|-----------|------|-----|------|------|-----|-----|
| Holotype | 1.4 | 1.0 | 1.3 | 1.0 | 1.2 | 2.5 |
| Paratype1 | 1.3 | 1.0 | 1.0 | 0.9 | 1.6 | 4.7 |
| mean of 2 | 1.35 | 1.0 | 1.15 | 0.95 | 1.4 | 3.6 |

XIII and XIV. Seminal vesicles 4 pairs, in IX-XII *F. fasciatus*

4. Spermathecal pores 3, midventrally, in 6/7, 7/8 and 8/9. Ventral surface in VII-IX tumid and with several longitudinal (glandular?) plications *F. sigillatus*
 Spermathecal pores 5, midventrally in 4/5 to 8/9. An oval, superficially pleated genital marking midventrally in VIII *F. menurus* sp. nov.

***Fletcherodrilus menurus* sp. nov.**
 (Figs 9; 10A, B; 11; 12)

TYPE LOCALITY

18°56'S, 146°13'E., Mt Spec National Park, North Queensland, under logs and rocks in rain-forest, K.R. McDonald, R.A. Atherton, 4.i.1977.

MATERIAL EXAMINED

HOLOTYPE: QMG211435.

PARATYPES: QMG211436-211441.

DESCRIPTION

Length 140-199mm, width (midclitellar) 6 mm, segments 202 (P6), 204 (P1). Form dorsoventrally slightly depressed. Pigmented purplish brown dorsally, buff ventrally. Prostomium epilobous 1/3- >1/2, closed, but with lateral margins continuing to 1/2 or 2/3 peristomium (sometimes flanked by other longitudinal furrows); it and entire body with a narrow mid-dorsal longitudinal groove (canalicula); prostomium also bisected ventrally (H, P1-6). First dorsal pore 5/6 (H, P1-6). Setae 40 (H), 36 (P1) in XII; 41 (H), 36 (P1) in XX; caudally, about 12 segments from posterior end, 44 (H, posterior amputee), 29 (P1); ventral gap not apparent in forebody, becoming recognisable on clitellum, not apparent far caudally; dorsal gap conspicuous but not large, and only slightly irregular, throughout. Setal ratios (Table 1).

Nephropores sporadically visible; in setal lines 14 in XIV; setal lines 7 in XVIII. Clitellum annular, greyish brown; 1/2XIII-XVIII, but interrupted ventrally in XIII, sometimes weakly developed dorsally to 1/2XIX; intersegmental furrows retained but not as sharp as elsewhere;

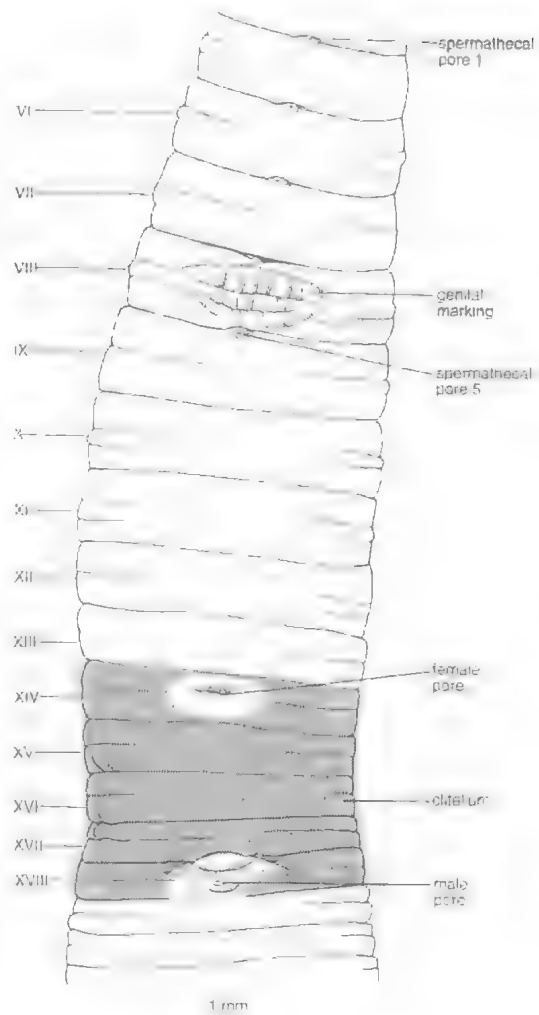


FIG. 11. *Fletcherodrilus menurus* sp. nov., paratype, QMG211436. Region of male and spermathecal pores, ventral view. Showing single male pore when male field is withdrawn.

dorsal pores occluded (H, P1). The male genital field shows two distinct forms which are here deduced from dissection to be stages in eversion. In the holotype, what may be termed the 'lyrate' condition obtains. Here the two minute male pores, posterior to the setal arc of XVIII and well median of setal lines *a*, being 0.4mm apart; each is connected by a short laterally running groove to a longitudinal groove which itself gives off short side branches. The longitudinal grooves are slightly convergent anteriad. The male pores and the system of grooves lie in an approximately circular depressed field which extends almost to the anterior border of XVIII, where it is bordered

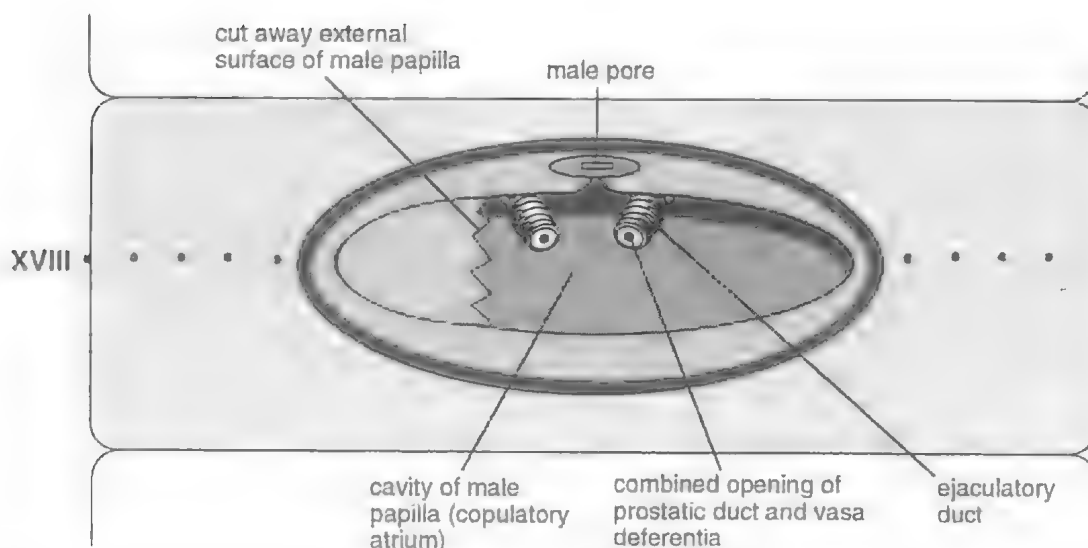


FIG. 12. *Fletcherodrilus menurus* sp. nov., paratype, QMG211441. Semidiagrammatic representation of dissection of male porophore by transverse incision, revealing internal bursa with two male pores.

by a semicircular rim, and extends onto the anterior region of XIX. In the other paratypes, in marked contrast, the male pore appears unpaired, midventral in the setal arc of XVIII, as a minute slit in a very small low, oval papilla. Transverse incision of the male papilla in paratype 6 (QMG 211441) reveals an inner cavity or bursa (Fig. 12) from the rear (dorsal) wall of which projects a pair of muscular ducts, the ectal end of the prostate ducts. It is therefore deduced that the lyrate condition is brought about by eversion of the dorsal wall of the bursa and that when this is retracted it leaves a single pore at the surface of the papilla. Accessory genital marking a large transversely oval pad midventrally in VIII, extending laterally to about setal lines 5, traversed by a deep furrow which coincides with the anterior margin of the setal annulus; longitudinal pleats arising from this furrow (P1 and paratypes 4-6; not present in holotype). Female pores paired, minute, immediately anteromedian to setae *a*, concealed in a transverse furrow which has tumid margins. Spermathecal pores 5, unpaired, midventral, in intersegmental furrows 4/5-8/9, each on a small, low oval papillae which creates a semicircular forward indentation of the furrow.

Last hearts in XII; those in X-XII latero-oesophageal. Supra-oesophageal vessel in X-XVI (H, P1). A subneural vessel present (P1). Gizzard large, elongate, and moderately firm, in

VI, deflecting the diaphanous septum 6/7 posteriorly; septum 5/6 very delicate and attached shortly anterior to middle of gizzard (H) or near its anterior rim (P1), giving the impression that this septum primitively passed to rear of gizzard; a wide, flaccid proventriculus present in segment IV. Oesophagus with circumferential vascular striae in IX-XVI, especially XII-XVI; in each of XIII, XIV and XV dilated on each side of dorsal vessel, and with moderately high radial laminae on its lateral walls; these dilations not constricted off from oesophageal lumen, but to be considered true calciferous glands. Intestinal origin in XVIII but in P1 not widening until XIX; typhlosole absent. Gut contents include large pieces of sclerophyllous leaves or vegetable fibres and quartz grains. Nephridia stomate, vesiculate holonephridia; bladders very large, elongate-fusiform wide, adiverticulate tubes, joined at ental extreme by nephridial duct, each ectally continued to pore as a long narrow duct; egress of ducts is near dorsal in II, slightly more ventral in III, and thereafter progressively more ventral until in anterior intestinal region it forms an irregular, ventrolateral or ventral line (H) or still far dorsal, though in slightly irregular longitudinal rows (P1). Holandric; small free funnels in X and XI; seminal vesicles on anterior septa of XI and XII, not subdivided into loculi (H) or also (pseudovesicles?) X, each with a few large loculi

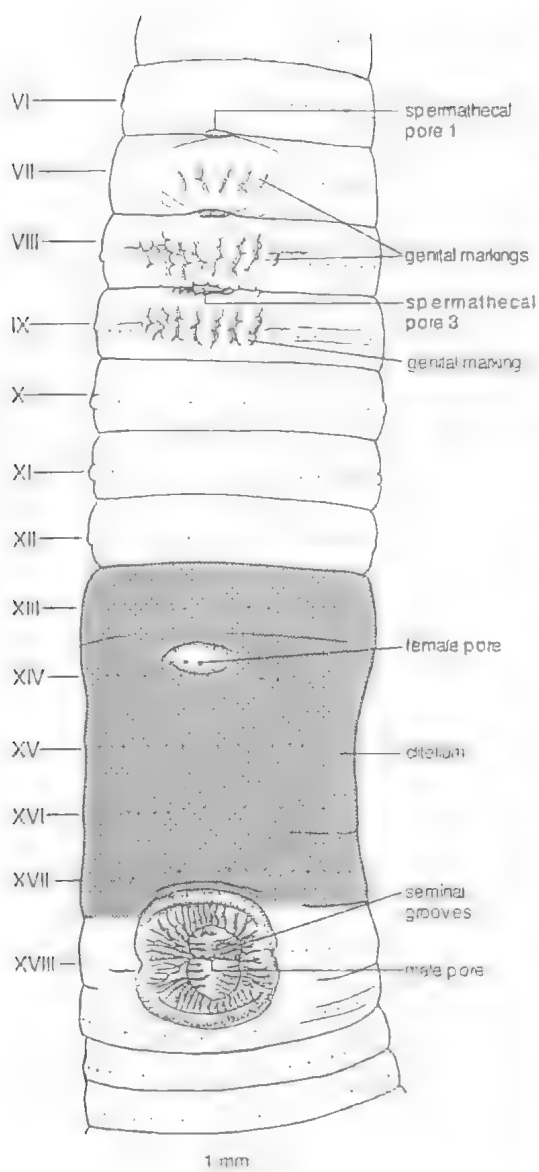


FIG. 13. *Fletcherodrilus sigillatus* (Michaelsen, 1916). Wallacha Falls. Region of male and spermathecal pores, ventral view.

(P1). Ovaries small masses with few large terminal oocytes in XIII (H), not developed in P1; ovisacs not recognisable. Prostates tubuloracemose, externally thickly tubular and smooth walled, restricted to XVIII in which they wind laterally from their ducts (H); right prostate compacted as a single large lobe with no subdivision (P1); each muscular duct widens in its

ectal half to form a bursa which is fused along most of its length to body wall; conjoined vasa deferentia of its side joining anteromedian limit of bursa (H, P1). Penial setae absent. Five unpaired spermathecae present, increasing size posteriad, each with large, irregularly ovoid ampulla, tapering duct and 2 tubular, tortuous, inseminated diverticula which enter body wall on either side of duct; ampullae lying to one or other side of ventral nerve cord and contralateral diverticulum passing under the cord; first three ampullae are on left and last two on right of the cord (H) or those of V and VIII, only, are on the left (P1).

ETYMOLOGY

From *Menura*, the lyre-bird, referring to the similarity of the configuration of the seminal grooves to the tail of this bird.

REMARKS

Fletcherodrilus menurus is clearly the sister-species of *F. sigillatus*. Both show a striking departure from the other species of *Fletcherodrilus*, *F. unicus* (Fletcher, 1889), *F. affinis* (Stephenson, 1933) and *F. fasciatus* (Fletcher, 1890), in the development of accessory genital markings and in the perichaetine condition of the setae. The genital markings consists of longitudinally pleated areas and are of a type unknown elsewhere. Development of these markings represents a remarkable apomorphic departure from the absence of markings throughout the remainder of the monophyletic *Fletcherodrilus-Terriswalkerius* clade. *F. menurus* is well defined from, and presumably plesiomorphic relative to, *F. sigillatus* in having 5 spermathecal pores in contrast with the 3 pores in the latter. Furthermore, the 'lyrate' condition of the putative seminal grooves of the male field in *F. menurus* differs from the anteroposteriorly duplicated, mirror image, array of grooves in *F. sigillatus*.

Dissection of the male porophore of a specimen with a single male pore, revealing two internal prostate pores (Fig. 12) is here considered to indicate that such specimens are conspecific with the externally lyrate holotype with its two male orifices. In the unlikely event of this being shown not to be the case, the name *F. menurus*, would be restricted to lyrate individuals.

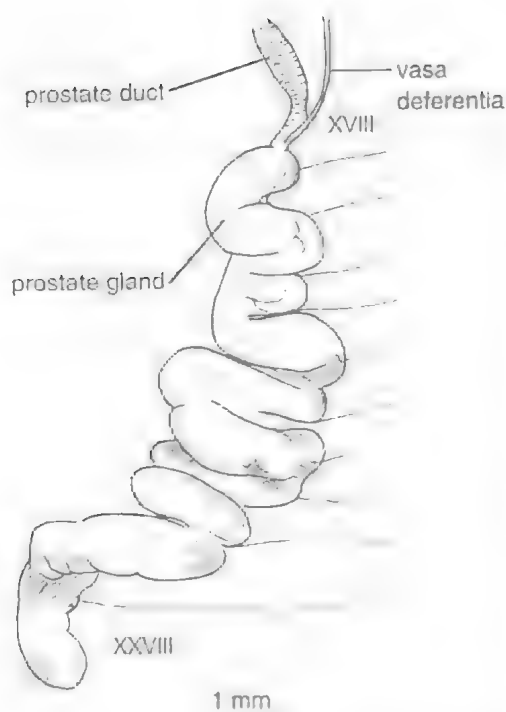


FIG. 14. *Fletcherodrilus sigillatus* (Michaelsen, 1916). Wallacha Falls. Right prostate.

***Fletcherodrilus sigillatus* (Michaelsen, 1916)**
(Figs 13; 14; 15)

Perionyx (Diporochaeta) sigillatus Michaelsen, 1916: 16-19, pl.1, figs 3, 4.

Diporochaeta sigillata; Jamieson, 1971c: 83.

Fletcherodrilus ? sigillatus; Jamieson, 1974a: 221.

Fletcherodrilus sigillatus; Jamieson, 1976b: 9.

TYPE LOCALITY

17°21'S.145°36'E., Malanda, in Cairns District, Qld.

MATERIAL EXAMINED

SYNTYPES: Royal Stockholm Museum, NHRS 1951. Zoology Museum, Hamburg, HMV8475.

OTHER RECORDS: 17°13'S.145°50'E., Wallacha Falls, Palmerston National Park, T. Walker, 1 specimen (Jamieson collection); 17°38'S. 145°32'E., Majors Mtn. N.E. Queensland, J. Covacevich, K. McDonald. R. Raven, QMGH1994 (ex QMGH1968); 17°17'S.145°37'E., Lake Eacham, closed forest, under sheet of corrugated iron, K. McDonald, J.D., 21.ix. 1974, QMG9000; 18°04'S. 144°52'E., 40 Mile Scrub, c. 62 km W Mt Garnet, under logs, R. Raven, QMGH1976; 17°23'S.145°39'E, Pelling's fragment

of rainforest, South of Tarzali, near Atherton, Craig Moritz, 18 Aug 1994, QM211455. All in Queensland.

DESCRIPTION

Length 101-170mm, width (midclitellar) 4.5mm, segments 148-(180?). Form dorsoventrally slightly depressed. Pigmented purplish brown to dark flesh coloured dorsally, pale, greyish ventrally. Prostomium epitanalylobous, it and entire body with a narrow middorsal longitudinal groove (canalicula). First dorsal pore 5/6 but an imperforate rudiment at 4/5. Setae 34/XII; 32/XX; caudally 38 (33/IX, 34/XII, XXII, 36/XXVI, Michaelsen); rows slightly more widely spaced ventrally than dorsally; ventral gap (*aa*) recognisable only behind clitellum, maximally (posteriorly) 2 *ab*; dorsal gap (*zz*) visible throughout, anteriorly = 2*zy*; posteriorly = 4 *zy* but narrowing posteriad as setae are more closely spaced caudally. Nephropores: a pair in each segment, commencing anteriorly in II, but forming an irregular sinuous line on each side, varying in position from near middorsum (in II) to dorsolateral, lateral, or ventrolateral and only occasionally symmetrically disposed in a segment. Clitellum annular, XIII, 1/2 XIII-1/2XXVII, XVII. Male pore unpaired, midventral equatorially in XVIII at bottom of a deep pit of specialized epithelium which extends anteriorly and posteriorly almost to setal arcs of XVII and XIX and laterally to setal lines 4-6, margin of pit slightly thickened and a little indented at setal arc of XVIII; bottom of pit in vicinity of male pore differentiated as an elliptical field, around pore, traversed by a conspicuous equatorial furrow in which male pore lies, this central field pleated by several, mostly transverse ridges; walls of pit with similar plications extending radially from central field. Discrete accessory genital markings absent but ventral surface in VII-IX tumid and with several longitudinal (glandular?) plications. Female pores paired, close together, shortly anteromedian of (or, Michaelsen, in front of) setae *a* of XIV. Spermathecal pores 3, unpaired, midventral, in 6/7, 7/8 and 8/9, each an eye-shaped aperture with tumid, almost papillate margins.

Last hearts in XII; those in X-XII latero-oesophageal. Supra-oesophageal vessel in IX-XIII; moderately developed. Gizzard large and moderately firm, in VI; septum 5/6 very delicate and attached near anterior limit of gizzard, giving the impression that this septum primitively passed to rear of gizzard; a wide, flaccid proventriculus present in the segment preceding

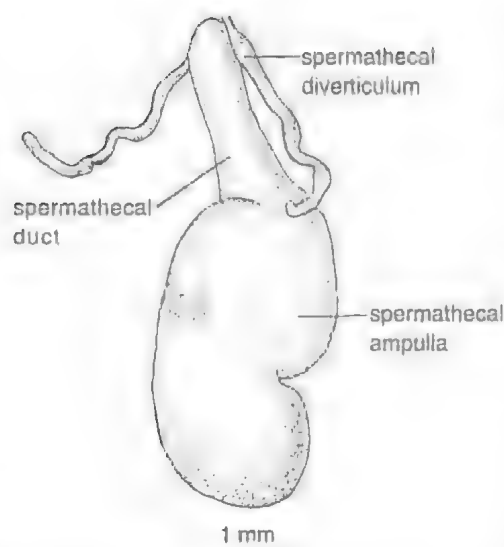


FIG. 15. *Fletcherodrilus sigillatus* (Michaelsen, 1916). Wallacha Falls, Spermatheca of IX.

gizzard. Oesophagus with circumferential vascular striae in IX–XVI; in each of XIII, XIV and XV dilated on each side of dorsal vessel, and with moderately high vertical laminae on its lateral walls; these dilatations not constricted off from oesophageal lumen, but probably to be considered true calciferous glands. Intestinal origin XVIII; typhlosole absent. Nephridia stomate, vesiculate holonephridia (funnels demonstrated for those discharging in II); bladders very large, elongate-fusiform wide, adiverticulate tubes, joined at ental extreme by nephridial duct, each ectally continued to pore as a long narrow duct which equals bladder in length only when pore is far dorsally. Holandric; funnels slightly iridescent in X and XI; gymnorchous; seminal vesicles racemose in XI and XII. Ovaries (webs of many oocytes) in XIII; rudimentary ovisacs in XIV. Prostates tubuloracemose, externally thickly tubular (c. 18 mm long and 0.7 mm wide, Michaelsen) and smooth walled, winding from XVIII to XXVII, each with a central lumen occupying a small fraction of total diameter (one eighth in middle of organ and with many lateral canals, Michaelsen); short but considerable muscular duct joined near glandular portion by vasa deferentia which then run distally in duct wall; transverse muscles present on body wall in vicinity of duct. Penial setae absent. Three unpaired spermathecae present, each with large,

flattened irregularly ovoid ampulla, well demarcated though stout duct and 2 tubular, tortuous diverticula which enter body wall on either side of duct; length spermathecae = 4 mm; ratio length: length duct = 2.7; ratio length: length diverticulum = 1.8.

REMARKS

All that remains of the single type-specimen in the Hamburg Museum, HM(V8475), is an isolated gizzard. Michaelsen reported that the type was strongly macerated and that he was unable to determine with certainty whether the anterior rudimentary seminal vesicles were in X or XI. He concluded that they were in XI but on this basis the gizzard appeared to be in VII, at which he expressed doubt. Calciferous glands were reported for XIV and XV, with a rudimentary pair, hardly to be considered glands, in XVI, and last hearts were stated to be in XIII. This sequence is one segment behind that of the new material dissected, from Wallacha Falls and 40 Mile Scrub, and Michaelsen's fear that it might be incorrect by one segment clearly was warranted.

Despite its perichaetine setal arrangement, Jamieson (1974a: 221) considered this species to be related to *Fletcherodrilus* rather than to *Perionychella* (i.e. *Diporochaeta*). Among its similarities with the three species already placed in *Fletcherodrilus* was the unpaired male and prostatic pores (a condition unknown in *Perionychella* but now known in *Terriwwalkerius mcdonaldii*), presence of calciferous glands in XIII–XV; intestinal origin in XVIII; the thickly tubular prostates; junction of the vasa deferentia with the prostate ducts well ectal of the glands; and the form of the spermathecae with their irregularly ovoid ampullae and digitiform diverticula at the body wall. The presence of diverticula on the nephridial bladders in the other species of *Fletcherodrilus* and their lumbricin setae cannot be considered significant obstacles to inclusion of *F. sigillatus* as these variations occur within *Diporochaeta*. The perichaetine condition is foreshadowed in *F. unicus* in which the posterior setal lines are sometimes irregular and there are occasionally supernumerary setae and a strongly perichaetine condition is now known for *F. menurus*.

Hiatidrilus gen. nov.

DIAGNOSIS

Setae 8 per segment. Male pores in XVIII. Genital markings present. Spermathecal pores 2

pairs, the last at anterior limit of IX. Gizzard large, in V. Oesophageal vascularization, with or without development of extramural calciferous glands, in the vicinity of the hearts. Intestine commencing in XV or XVI. Nephridia stomate holonephridia, with or without bladder-like ducts. Holandric or metandric. Ovaries in XIII. Prostates coiled tubular (or tubuloracemose?). Penial setae present. Spermathecae each with 2 clavate diverticula.

DESCRIPTION

Setae 8 per segment. Dorsal pores present. Clitellum annular or saddle-shaped, in the vicinity of XIII-XVII. Male pores in XVIII, median or lateral of *b* lines. Segmental and intersegmental genital markings present. Spermathecal pores 2 pairs, in or immediately behind 7/8 and 8/9 in *b* lines. Female pores anteromedian or anterior to setae *a* of XIV. Last hearts in XII. Gizzard large, in V. True extramural, pyriform, dorsolateral calciferous glands two pairs, in XI and XII; or oesophagus segmentally dilated and vascular, with large internal villi in IX-XIII but lacking calciferous glands. Intestine commencing in XV or XVI. Nephridia stomate, avascular holonephridia; ducts discharging in *c* to *cd* lines, slender or wide and bladder-like. Testes in X and XI or XI only. Ovaries and funnels in XIII; ovisacs absent; pseudovesicles absent or present in XIV. Prostates tubular, much wound, in XVIII and XIX. Penial setae present. Spermathecae each with 2 clavate diverticula.

DISTRIBUTION

Bunya Mountain (South-east Queensland) and Grafton, on the Clarence River (New South Wales).

TYPE SPECIES

Diporochaeta bunya Jamieson, 1976b.

SPECIES INCLUDED

Diporochaeta bunya Jamieson, 1976b; *Cryptodrilus semicinctus* Fletcher, 1890

KEY TO SPECIES OF HIATIDRILUS

- 1, Holandric, with two pairs of male funnels. Genital markings a midventral transverse glandular pad occupying the region in front of the male pores, extending longitudinally from 1/2XVII-1/2XVIII and laterally to include setae *b* of XVII, bearing on each side, a circular whitish genital marking in *b* posteriorly in XVII, and a further one median to setal lines *a* at the site of

the obliterated intersegment 17/18; a further similar pair of circular genital markings present at the anterior border of XIX behind the latter pair, median of *a* lines, each of this pair on an elliptical tumescence extending longitudinally from 1/2XVIII to include setae *ab* of XIX, furrow 18/19 persistent and separating off its anterior region; each ellipse conjoined with that of the other side to form a transverse pad narrowed in the midline. A transversely elliptical tumid pad present midventrally in each of XI and XII filling the segment and including setae *a*, each pad with a pair of circular genital markings median to *a*, the marking on the right in XII may be transversely duplicated *H. bunya*

Metandric, with male funnels in XI only. Genital markings at fullest development small circular boss-like prominences, each surrounded by an elliptical glandular field, unpaired and midventral in 13/14; paired between setae *a* in 14/15, 15/16, and 16/17, those in 14/15 almost contiguous medianly, those in the next two intersegments further apart so that those of 16/17 are shortly median of setae *a*; a small marking on each side in front of and behind the male porophore, lateral of *b* lines, at the posterior and anterior limits of XVII and XIX respectively; paired markings almost contiguous medianly in 19/20 accompanied by a marking in *ab* (the left one bearing a boss); and an unpaired median marking in 20/21. Further genital markings present in the vicinity of the spermathecal pores in or lateral of the lines of ventral setal couples: post-setal in VII and VIII, pre-setal in IX and X, those on the right side transversely duplicated in VII and triplicate in VIII; an additional equatorial marking present on this side in VIII. Additionally the posterior genital field (XIII posteriorly) may be similar though several markings are at least unilaterally absent. Constant are the paired markings at 14/15, 15/16, 16/17, posterior XVII and anterior XIX. The anterior genital markings may be absent *H. semicinctus*

ETYMOLOGY

Hiatidrilus, meaning 'gap worm', referring to its intermediate location between southern *Diporochaeta*s and *Terrisswalkerius*.

REMARKS

The name *Hiatidrilus* refers to the fact that the two known species of this genus, previously referable to *Diporochaeta*, lie in the southern region of the very large geographical hiatus which separates *Diporochaeta*, in Victoria and Tasmania, from the North Queensland species of *Diporochaeta* which have here been transferred to *Terrisswalkerius*.

Presence of two spermathecal diverticula, on opposite sides of the duct, separates this genus from all species of *Diporochaeta* s. lat., excepting the Tasmanian *D. scolecoidea*. The latter species differs significantly in being strongly perichaetine and in having racemose prostates. A supernumerary diverticulum in series with the usual diverticulum occasionally occurs in *D. hobartensis* (Tasmania), and the diverticulum is doubled in *D. willsiensis* (Victoria) but although these two species also have basically eight setae per segment, they have five pairs of spermathecae. A highly distinctive feature of *Hiatidrilus bunya* relative to most *Diporochaeta* species is the possession of true extramural calciferous glands, in XI and XII, although extramural glands occur in the type species, *D. intermedia*, in X and XI. *H. semicinctus* is distinguished in being metandric and having a saddle-shaped clitellum. A detailed account of the distinctive genital markings is given in the key in the absence of specific descriptions.

The two species here referred to *Hiatidrilus* could be placed in separate genera but their differences can reasonably be accommodated in a single genus. The phylogenetic analysis supports their congeneric status. The Bunya Mountains location of *H. bunya* is near the source of the Clarence River by which *H. semicinctus* occurs, giving some geographical validity to recognition of a special relationship between the two species.

Hiatidrilus bunya
(Jamieson, 1976b) comb. nov.

Diporochaeta bunya Jamieson, 1976b: 18-20, figs 1, 11a, 13e, 15e, table 1

TYPE LOCALITY

26°57'S.151°35'E., Bunya Mts., near Festoon Falls-Qld.

MATERIAL EXAMINED

HOLOTYPE: QMG8336.

REMARKS

H. bunya is distinguished from *H. semicinctus* in the key.

Hiatidrilus semicinctus
(Fletcher, 1890) comb. nov.

Cryptodrilus semicinctus Fletcher, 1890: 996-997.

Megascolides semicinctus Beddard, 1895: 494.

Plutellus semicinctus Michaelsen, 1900: 170; Jamieson, 1971c: 88.

TYPE LOCALITY

29°41'S.152°56'E., Grafton, Clarence River-NSW.

MATERIAL EXAMINED

SYNTYPES: AMW1312 (3 specimens; a fourth is in fact a *Heteroporodrilus*).

REMARKS

H. semicinctus is distinguished from *H. bunya* in the key.

CLADISTIC ANALYSIS

MATERIALS AND METHODS

Twenty nine external and internal characters, representing most features used in megascolecid taxonomy, were listed in a data matrix for 39 species of the tribe Perionychini. These included the type species of all Australian perionychins and the New Zealand type-species of *Diporochaeta*, *D. intermedia*.

Species selected and sources of data were as follows (asterisked species are the type-species of their respective genera):

Diporochaeta capensis: (Jamieson, 1974a); **Diporochaeta intermedia*: Jamieson, 1976a; *Diporochaeta kershawi*: (Jamieson, 1974a); *Diporochaeta mortoni* (Jamieson, 1974a); *Diporochaeta victoriae* (Spencer, 1892a; Jamieson, unpubl.); *Fletcherodrilus menurus* sp. nov.; *Fletcherodrilus sigillatus*: this account; **Fletcherodrilus unicus*: Jamieson & Wampler, 1979; **Gratiophilus georgei* Jamieson, 1971b; *Heteroporodrilus* sp.; **Heteroporodrilus tryoni* Jamieson, 1970a; **Hiatidrilus* (= *Diporochaeta*) *bunya* (Jamieson, 1976b); *Hiatidrilus* (= *Diporochaeta*) *semicinctus* (Fletcher, 1890; Jamieson, unpublished); **Paraplutellus insularis* Jamieson, 1972a; **Perionychella dendyi* (Spencer, 1892b); **Pinguidrilus tasmanianus* Jamieson, 1974a; **Plutellus heteroporus*: Jamieson, 1971d; **Pseudoperichaeta smithi*: Jamieson, 1970a; **Simsia tuberculata*: Jamieson, 1972a, b; **Woodwardiella callichaeta*: Jamieson, 1970a; and the following *Diporochaeta* species here transferred to *Terriswalkerius*: *D. atavius*: Jamieson, 1976b, unpubl.; *D. athertonensis*: Jamieson, 1976b, and this account; *D. barronensis*: Jamieson, 1976b; *D. blounti* Jamieson, 1976b; **D. canaliculatus*:

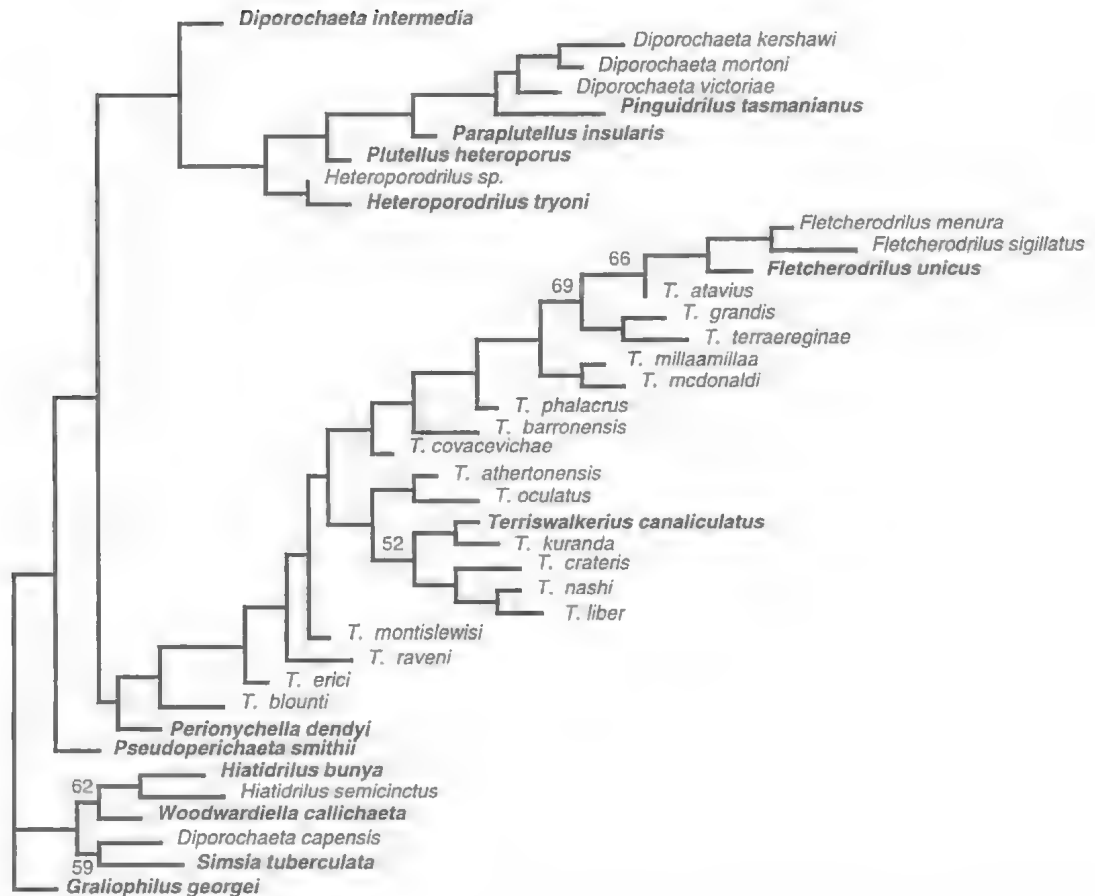


FIG. 16. 50% majority rule consensus tree of 29 equally and most parsimonious trees for the genera of Perionychini, including all known species of *Terriswalkerius*, resulting from an heuristic search (see text).

Jamieson, 1976b; *D. crateris* Jamieson, 1976b; *D. erici*: Jamieson, 1976b; *D. grandis*: Jamieson, 1976b; *D. kuranda*: Jamieson, 1976b; *D. millaamillaa* Jamieson, 1976b; *D. montislewisi* Jamieson, 1976b; *D. nashi* Jamieson, 1976b, and this account; *D. oculata* Jamieson, 1976b; *D. phalacrus* (Michaelsen, 1916; and Jamieson, unpubl.); *D. raveni* Jamieson, 1976b; *D. terraereginae*: Jamieson, 1974b; *Terriswalkerius covacevichae* sp. nov.; *Terriswalkerius liber* sp. nov.; *Terriswalkerius mcdonaldi* sp. nov.

The characters used were as follows:

[1]Body canaliculate: (0) no, (1) yes,

[2]First dorsal pore, at anterior limit of segment: (0) absent, (1) 4, (2) 5, (3) 6, (4) 7, (5) 8, (6) 9, (7) 10, (8) 11, (9) further posteriad,

[3]Setal arrangement: (0) lumbricin, (1) perichaetine,

[4]Nephropore rows: (0) regular, (1) irregular, (2) with complex alternation,

[5]Clitellum, first full segment: (0) 12, (1) 13, (2) 14, (3) 15,

[6]Male pores: (0) single, (1) paired,

[7]Male pores, setal location: (0) median to *a*, (1) *a*, (2) *ab*, (3) *b*, (4) *bc*, (5) *c*, (6) *cd*, (7) *d*, (8) dorsal of *d*,

[8]Female pores: (0) single, (1) paired, (1) Invariable)

Fig. 17. Input Data Matrix

| Node | 111111111222222222 |
|---------------------|-------------------------------|
| | 12345678901234567890123456789 |
| D. intermedia | 0010218110410111211510101000 |
| H. bunya | 04002121102302112131502101110 |
| F. menurus | 13112001105012132220810121001 |
| F. sigillatus | 13111001103212112220810121100 |
| D. kershaw | 02001111105001112120702100110 |
| F. unicus | 12002001005012112230811121001 |
| G. georgei | 02001121102301113130902101000 |
| D. capensis | 23122131102301132110602101010 |
| P. heteroporus | 04021132105101112131510100100 |
| H. sp. | 03022131103201113131510101002 |
| H. tryoni | 03022121103202313131510101000 |
| Paraplutellus fn. | 04022131105001112201611100010 |
| Pinguiculus tas. | 0801212110500023130910100010 |
| Pseudoperichaeta s. | 01012121104101112130902102000 |
| S. tuberculata | 01002121112301212130802100010 |
| W. callichaeta | 29002121102301172120202102010 |
| P. mortoni | 22001121105001112130811100110 |
| D. victorae | 14002121105001112130711100100 |
| H. semicinctus | 09002141102302112130600230110 |
| T. atavus | 271121020050022222222222222 |
| T. athertonensis | 13101101003201112130610101000 |
| T. barronensis | 12102161003001132230811120000 |
| T. blounti | 22101131001301112130702101000 |
| T. canaliculatus | 13112171003201112230710181000 |
| T. crateris | 011221510012113122110101000 |
| T. erici | 12111111004101112130811101000 |
| T. grandis | 12112121005001112131700101000 |
| T. kuranda | 13112151004101112230710161100 |
| T. millaamillaa | 12102101004101112230800180000 |
| T. montislewisi | 12102131003001112230711101100 |
| T. nashi | 13101151001401112230710101000 |
| T. oculatus | 12101141003202412220710101000 |
| T. phalacrus | 131221100500212231001121000 |
| T. raveni | 12102161003001112120711110100 |
| T. terraereginae | 12112111004001113130802161000 |
| T. mcdonaldii | 02102101004101112231001121000 |
| T. covacevichae | 1310212003101112230911101100 |
| T. liber | 13102112001401132130710170100 |
| P. dendyl | 01102131104101112130900142100 |

[9]Accessory genital markings: (0) absent, (1) present,

[10]Spermathecal pores location: (0) intersegmental, (1) significantly segmental,

[11]Spermathecal pores, number of segments: (1) 1, (2) 2, (3) 3, (4) 4, (5) 5,

[12]Spermatheca first: (0) 5, (1) 6, (2) 7, (3) 8, (4) 9,

[13]Spermathecal pores, pairing: (0) paired, (1) single,

[14]Spermathecal diverticula: (0) absent, (1) 1, (2) 2, (3) 3, (4) >3,

[15]Spermathecal diverticula: (0) absent, (1) uniloculate, (2) multiloculate, (3) branched, (4) bifid,

[16]Spermathecal diverticula, length: (0) absent, (1) <ampulla+duct, (2) =ampulla+duct, (3) >ampulla+duct,

[17]Last hearts in segment: (0) 10, (1) 11, (2) 12, (3) 13,

[18]Gizzard segment: (0) absent, (1) 5, (2) 6, (3) 7,

[19]Gizzard, development: (0) absent, (1) weak, (2) moderate, (3) strong,

[20]Calciferous glands extramural to oesophagus: (0) absent, (1) present,

[21]Intestinal origin: (0) 10, (1) 11, (2) 12, (3) 13, (4) 14, (5) 15, (6) 16, (7) 17, (8) 18, (9) 19,

[22]Nephridial bladders: (0) absent, (1) present,

[23]Nephridial diverticula: (0) absent, (1) present,

[24]Male funnels: (0) proandric, (1) holandric, (2) metandric,

[25]Seminal vesicles, segments: (0) 9,12, (1) 9,10,11,12, (2) 11,12, (3) 12, (4) 9,10,12, (5) absent, (6) 8,9,12, (7) 12,13, (8) 11,12,13, (9) 9,12,13,

[26]Prostate type: (0) tubular, (1) tubuloracemose, (2) racemose,

[27]Prostate, extent: (0) restricted to segment 18, (1) not restricted to 18,

[28]Penial setae: (0) absent, (1) present,

[29]Prostatic bursa: (0) absent, (1) present,
Of these, character 8 was constant, and 24 was uninformative, neither therefore contributing to the phylogeny.

The input data matrix is presented in Fig. 17.

SEARCH OPTIONS

The analysis was performed using PAUP, version 3.0s, of Swofford (1993). Because of the inordinate time needed for branch and bound searching, the heuristic search option was

employed with the following search settings: addition sequence: simple; 1 tree(s) held at each step during stepwise addition; tree-bisection-reconnection (TBR) branch-swapping performed; MULPARS option in effect; steepest descent option not in effect; initial MAXTREES setting = 900; branches having maximum length zero collapsed to yield polytomies; topological constraints not enforced; trees unrooted; multi-state taxa interpreted as polymorphism.

A principle underlying the analysis was that of 'pattern cladism' in which a priori evolutionary assumptions are minimised. Accordingly, no attempt was made to establish transformation series, and polarity, for each character. Character states were often placed in purely arbitrary order and the characters were run "unordered". However, the plesiomorph condition was implied, and symplesiomorphic matching avoided, by employment of an outgroup. This was selected as the apparently relatively plesiomorphic taxon *Graliophilus georgei*.

RESULTS

Heuristic searching under these conditions resulted in 29 equally and most parsimonious trees: tree length = 213; consistency index (CI) = 0.521; homoplasy index (HI) = 0.714; excluding uninformative characters, CI = 0.420, HI = 0.717; retention index (RI) = 0.626; rescaled consistency index (RC) = 0.326. The 29 trees are summarized in Fig. 16.

DISCUSSION

In an 'intuitive' systematic study in the first part of this paper it has been concluded that the North Queensland species of *Diporochaeta*, with *Fletcherodrilus*, form a monophyletic group, diagnosed inter alia by loss of accessory genital markings, and that this warrants separate generic status, as the new genus *Terrisswalkerius*. It has also been concluded that *Fletcherodrilus* represents an apomorphic clade (but not necessarily the sister-group) of this assemblage but that, at least for convenience, this should be retained as a separate genus. It has further been determined that the Bunya Mountains isolate of *Diporochaeta* merits separate generic status, as *Hiaudrilus bunya*, and that *Cryptodrilus semicinctus* Fletcher, 1890, from Grafton, on the Clarence River, New South Wales, is congeneric with it. It was suspected that implementation of these conclusions would leave the residue of

Diporochaeta as a paraphyletic entity requiring further resolution. It was also considered that if *Fletcherodrilus* were a terminal, apomorphic clade of the *Fletcherodrilus-Terrisswalkerius* assemblage, only this joint assemblage would be a monophyletic whole and that separation of *Fletcherodrilus* would render *Terrisswalkerius* paraphyletic.

The cladistic analysis was instigated to test these taxonomic decisions and to investigate wider relationships of the above genera with the other Perionychini. To this end, the New Zealand type-species of *Diporochaeta*, *D. intermedia*, was included in the analysis, in addition to species of these genera, as were the type-species of every Australian perionychin genus. Some additional species were included in the analysis.

The phylogram resulting from the cladistic analysis (Fig. 16) allows discussion of the above systematic conclusions. The *Terrisswalkerius-Fletcherodrilus* assemblage is indeed a monophyletic entity, with *Fletcherodrilus* forming a terminal, monophyletic clade, and separation of *Fletcherodrilus* as a distinct genus is shown to result in a paraphyletic *Terrisswalkerius*. The assemblage is defined by the synapomorphy loss of accessory genital markings (and intestinal origin in XVII). *Fletcherodrilus* forms an apomorphic, terminal clade in which the spermathecal and male pores have united midventrally, the spermathecal condition being a homoplasy with *T. mcdonaldi*, and, less significantly, the seminal vesicles have come to occupy segments XI and XII. *F. sigillatus* and *F. menurus* have departed from the condition in the type-species, *F. unicus*, and all *Terrisswalkerius* species, in which accessory genital markings are apomorphically absent, by developing a distinctive type of pleated genital markings ventrally in the vicinity of the spermathecal pores.

A striking feature of the phylogram is that the type-species of *Diporochaeta*, *D. intermedia*, is separated by other genera from those *Diporochaeta* species here assigned to *Terrisswalkerius* and, indeed, from all other *Diporochaeta* species included in the analysis. It is not suggested that this preliminary analysis gives a definitive phylogenetic placement for *D. intermedia*, but separation of *Terrisswalkerius* from *Diporochaeta* s. strict. is clearly justified. However, the analysis suggests that *Perionychella* Michaelsen, 1907, as exemplified by its type-species, *P. dendyi* (Spencer, 1892b), is the sister-taxon of the *Terrisswalkerius-*

Fletcherodrilus assemblage, from which it differs notably in having developed racemose prostate glands. The unifying apomorphy between *Perionychella* and this assemblage, extension of the prostates through more than one segment, is, however, very tenuous and is of doubtful significance.

The phylogram separates the remaining perionychin genera from *Diporochaeta* as typified by *D. intermedia*. It suggests that the genus *Perionychella*, currently subsumed in *Diporochaeta*, is the sister-taxon of the *Terrisswalkerius-Fletcherodrilus* assemblage. It is not inconsistent with the generic status of the other perionychin genera, *Gratiophilus*, *Heteroporodrilus*, *Paraplutellus*, *Perionychella*, *Pinguidrilus*, *Plutellus*, *Pseudoperichaeta*, *Simsia*, and *Woodwardiella*, but significant autapomorphies remain to be established for some of these. Where genera are not monotypic this will require inclusion of more than one species from each genus, a procedure beyond the scope of the present study.

The phylogram also supports the decision to place *Cryptodrilus semicinctus* Fletcher, 1890, with *Diporochaeta bunya* Jamieson, 1976b, in the new genus *Hiatidrilus*, the two being united by the synapomorphic doubling of the spermathecal diverticula. However, *H. semicinctus* remains a very discrete perionychin in being metandric and having a saddle-shaped clitellum. *Hiatidrilus* forms a clade with *Woodwardiella callichaeta* and *Simsia tuberculata*, the type-species of their genera, and with *Diporochaeta capensis*, on three tenuous characters, which are homoplasie with other species. These are location of the first dorsal pore in intersegmental furrow S/6, supposed forward movement of the intestinal origin to XVI and the presence of penial setae. *Simsia* is defined, as when erected, by the multiloculate condition of the spermathecal diverticula which is unique for the species computed, and by three homoplasie characters, including the putative development of tubular, from tubuloracemose, prostates.

Separation of *Diporochaeta kershawi*, *D. victorlae* and *D. (=Perionychella) mortoni* from *Diporochaeta s. strict.* is supported by the phylogram (Fig. 16) and the generic status of these species requires further consideration. However, their inclusion, with *Pinguidrilus*, in a clade which includes basally *Heteroporodrilus*, *Plutellus* and *Paraplutellus*, is probably artefactual. The latter three genera have long been regarded, and I consider correctly, as a

homogenous entity in the very distinctive complex alternation of their nephropores and the strong development of their calciferous glands. *Pinguidrilus* has a unique apomorphy, within the taxa included in the analysis, of loss of spermathecal diverticula.

Within *Terrisswalkerius*, of which all known species are included in the cladistic analysis (Fig. 16), the most plesiomorphic species appears to be *T. blounti*, but this has undergone a major apomorphy in reduction of the spermathecae to a single segment, this being VIII. At the other extreme, *T. atavicus*, is the most derived species and forms the sister-taxon of *Fletcherodrilus* with which its only notable synapomorphy is duplication of the spermathecal diverticulum. It shows no apomorphies over its ancestor which is shared with *T. grandis* and *T. terraereginae*. These two species are tenuously linked by the synapomorphies of location of male pores in setal lines *ab* and of the gizzard in segment V, both homoplasie conditions. Other pairs of sister-species are: *T. millaamillau* and *T. mcdonaldi* (as predicted in the systematics section), *T. athertonensis* and *T. oculatus*, *T. kuranda* and *T. canaliculatus*, and, again as suggested above, *T. nashi* and *T. liber*. Although the synapomorphies within each pair of species may seem of questionable significance, generation of the pairs in the context of the complete set of data and of the tree warrants serious consideration of the relationship indicated. The pairing of the undoubtedly extremely close if not conspecific *T. nashi* and *T. liber* gives substance to this argument. Whereas some species of *Terrisswalkerius* form paraphyletic series, within the *Terrisswalkerius* section of the *Terrisswalkerius-Fletcherodrilus* assemblage, a striking monophyletic species group is observable, consisting of *T. athertonensis*, *T. oculatus*, *T. canaliculatus*, *T. kuranda*, *T. crateris*, *T. nashi* and *T. liber*. For the same reasons this grouping deserves further consideration though it is based on only two, apparently weak synapomorphies, location of the first clitellar segment at XIII, and development of tubular, from tubuloracemose prostates, both of which are homoplasie states.

ACKNOWLEDGEMENTS

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THE ULTRASTRUCTURE OF SPERMATOZOA OF THE AUSTRALIAN SKINKS,
CTENOTUS TAENIOLATUS, *CARLIA PECTORALIS* AND *TILIQUA SCINCROIDES SCINCROIDES* (SCINCIDAE, REPTILIA).

B.G.M. JAMIESON AND D.M. SCHELTINGA

Jamieson, B.G.M. & Scheltinga D.M. 1994 12 01: The ultrastructure of spermatozoa of the Australian skinks, *Ctenotus taeniolatus*, *Carlia pectoralis* and *Tiliqua scincoides scincoides* (Scincidae, Reptilia), *Memoirs of the Queensland Museum* 37(1):181-193. Brisbane. ISSN 0079-8835.

Spermatozoa of *Ctenotus taeniolatus*, *Carlia pectoralis* and *Tiliqua scincoides scincoides* are filiform, and approximately 84.0µm, 96.5µm and 57.5µm long, respectively. The acrosome vesicle is in the form of a hollow, concentrically zoned cone which basally overlies a paracrystalline subacrosomal cone which invests the tapered anterior end of the nucleus. The perforatorium is a slender rod extending anteriorly from the subacrosomal material. *Ctenotus* and *Tiliqua* resemble each other and differ from *Carlia* in the following respects: (1) acrosome elongate (relatively short in *Carlia*); (2) acrosome depressed near its tip; (3) perforatorium strongly oblique (very slightly oblique in *Carlia*); (4) a conspicuous laminated structure on each side of the proximal centriole (absent in *Carlia*); (5) midpiece with four dense ring structures in longitudinal succession (in *Carlia* mitochondrial transformations are scattered irregular dense bodies of varying sizes); (6) mitochondria between the mitochondrial transformations form slightly sinuous columnar structures, in the order of 10 in transverse section, with numerous predominantly longitudinal cristae (in *Carlia* mitochondria are elongate, tubular structures, with indistinct cristae, which weave between the intermitochondrial bodies); (7) enlargement of the peripheral fibres adjacent to doublets 3 and 8 but not the gross enlargement which occurs in the anterior region of the axoneme in *Carlia*. In all three genera the midpiece terminates with an annulus; peripheral dense fibres are associated with the 9 triplets of the distal centriole and the doublets of the axoneme within the midpiece; only those peripheral fibres adjacent to doublets 3 and 8 remain conspicuous to the level of the annulus, each as a double structure associated with the annulated fibrous sheath; and all peripheral fibres are absent from the principal piece. The close similarity of the sperm of *Tiliqua* (in the *Egernia* group) to those of *Ctenotus* and *Nangura* (in the *Sphenomorphus* group) indicates that these groups form a monophyletic entity while the differences of the sperm of *Carlia* suggest that its *Eugongylus* group is less closely related. □ *Ctenotus taeniolatus*, *Carlia pectoralis*, *Tiliqua scincoides scincoides*, Scincidae, Reptilia, spermatozoon, ultrastructure, phylogeny.

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Published descriptions of the male gametes of the Scincidae are limited to: a description of the mature spermatozoon of *Chalcides ocellatus tiligugu* by Furieri (1970); an account of spermiogenesis, with some description of mature, epididymal sperm, in the same subspecies by Carcupino et al. (1989); a very brief account of the development of the midpiece in *Eumeces laticeps* by Okia (1990); and a description of mature sperm of *Nangura spinosa* (a genus and species recently erected by Covacevich, et al., 1993) by Jamieson & Scheltinga (1993). The latter paper lists all published references to the ultrastructure of spermatozoa or spermiogenesis in reptiles.

Greer (1979) separated the Australian Scincidae into three phylogenetic groups: The

Sphenomorphus group (includes *Ctenotus*), *Eugongylus* group (includes *Carlia*) and *Egernia* group (includes *Tiliqua*).

MATERIALS AND METHODS

The testis and ducts of the Copper-tailed skink, *Ctenotus taeniolatus* (White, 1790) and the Rainbow skink *Carlia pectoralis* (De Vis, 1885) were dissected from a single euthenased specimen of each species. A portion of one duct was biopsied from a single specimen of Blue-tongued skink, *Tiliqua scincoides scincoides* (White, 1790), which was later released. *Ctenotus taeniolatus* and *Carlia pectoralis* were collected from Hervey Bay, Southeastern Queensland (SEQ). *T. scincoides* was collected from the Brisbane sub-

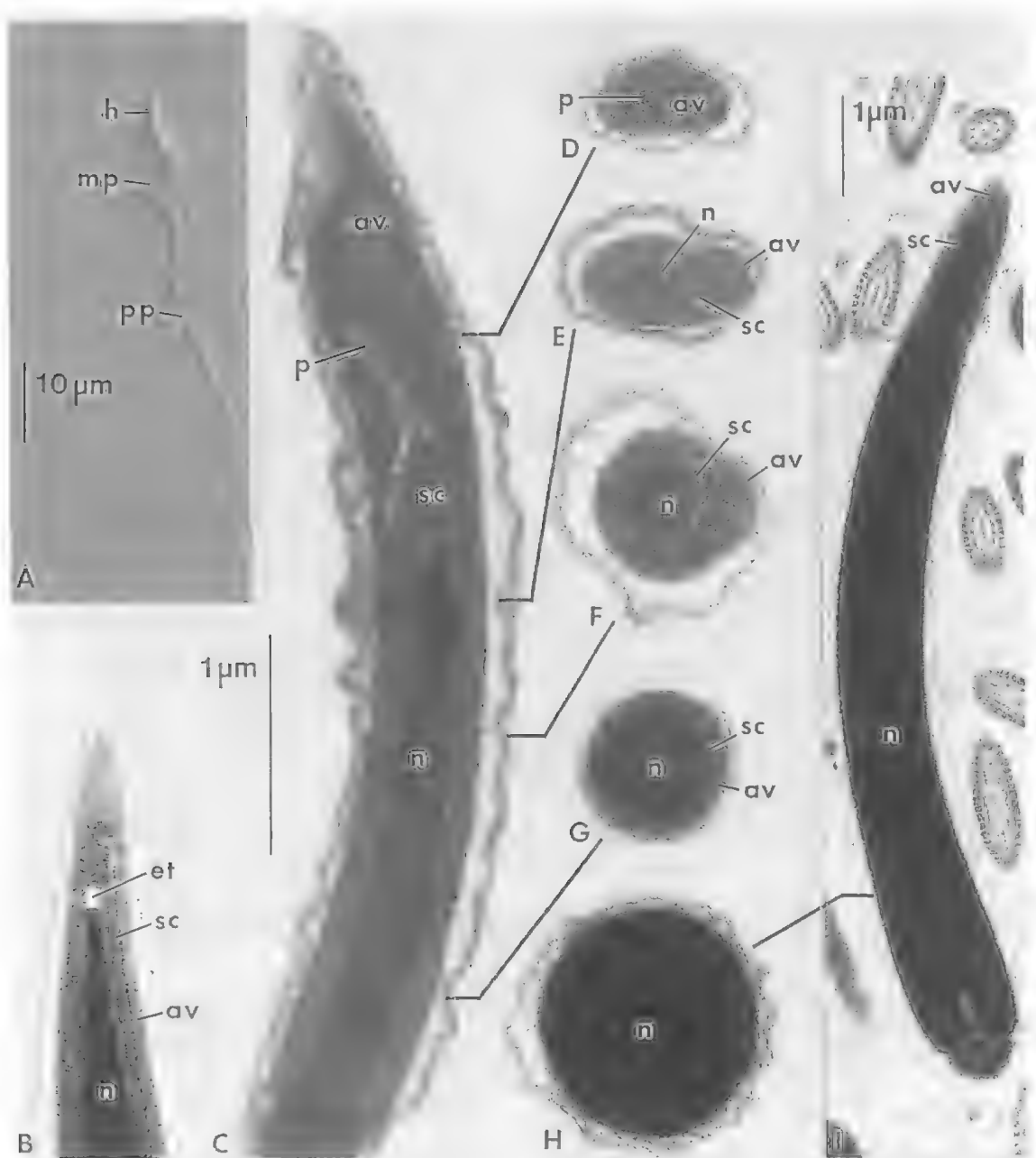


FIG. 1. *Ctenotus taeniolatus*. A, whole spermatozoon (Nomarski contrast light microscopy); B, longitudinal section (L.S.) through the nuclear point showing the epinuclear electron lucent region; C, L.S. through the acrosome showing the nuclear point and that the longitudinal axis of the perforatorium appears to be slightly oblique relative to that of the acrosome vesicle; D-G, a series of transverse sections (T.S.) through the acrosome (Note that anteriorly, in D and E, the acrosome is depressed in transverse sections, while further posteriorly, in F, it is unilaterally ridged, and at its posterior limit, in G, it is circular); H, T.S. through the nucleus. I, L.S. through the length of the nucleus. B-H to the same scale, as indicated. Abbreviations: a = acrosome; av = acrosome vesicle; et = epinuclear electron lucent region; mp = midpiece; n = nucleus; p = perforatorium; pm = plasma membrane; pp = principal piece; sc = subacrosomal cone.

urb of Indooroopilly, SEQ. The tissues were diced into 1-2mm³ portions, and fixed for transmission electron microscopy (TEM), in 3% glutaraldehyde in 0.1M sodium phosphate buffer (pH 7.2), at 4°C for 2 hours, being agitated for the first hour. The material was then rinsed in 0.1M phosphate buffer; post-fixed for 80 min in similarly buffered 1% osmium tetroxide; rinsed in buffer; dehydrated through an ascending ethanol series; and infiltrated and embedded in Spurr's epoxy resin. Sections were cut with diamond knives, on an LKB 2128 UM IV microtome. Thin sections, 50-80nm thick, were collected on carbon stabilized, collodion-coated, 200µm mesh copper grids, rinsed in distilled water, stained for 30s in Reynold's lead citrate, then in 6% aqueous uranyl acetate for 1-4 mins and for a further 1-2 mins in lead citrate before final rinsing. Electron micrographs were taken on an Hitachi 300 electron microscope at 75kV and a JEOL 100-s electron microscope at 60kV. Light microscopic observations of spermatozoa, from glutaraldehyde-fixed tissue squashes, were made under Nomarski contrast using an Olympus BH2 microscope.

RESULTS

Spermatozoa of *Ctenotus taeniolatus*, *Carlia pectoralis* and *Tiliqua scincoides scincoides* are filiform, and approximately 84.0µm, 96.5µm (mean of 4, S.D = 7.1) and 57.5µm long (mean of 2, S.D = 3.6), respectively. Dimensions (for one or two sperm of *Ctenotus taeniolatus*, *Carlia pectoralis* and *Tiliqua scincoides scincoides*, respectively) are: 5.3µm, 2.3µm and 4.1µm for the length of the acrosome complex; 6.8µm, 2.9µm and 5.1µm for the nucleus posterior to the acrosome; 7.1µm, 11.5µm and 5.5µm for the midpiece, from transmission electron microscopy, and, from light microscopy 64.8µm, 79.8µm and 42.8µm for the flagellum behind the midpiece (principal piece) (Figs 1-6).

The head (acrosome and nucleus), and often the midpiece and flagellum, is curved (Figs 1A; 3A,B; 5A). As a result of this curvature in the spermatozoa of *Ctenotus* and *Tiliqua* it has not been possible to obtain a complete longitudinal section through the head. The sperm of all three skinks are circular in cross section with the exception of the acrosome of *Ctenotus* and *Tiliqua*. Although the acrosome of these two species is circular at its base, anterior to this *Ctenotus* sperm develops a unilateral ridge and from the tip of the nucleus it becomes increasingly depressed in the

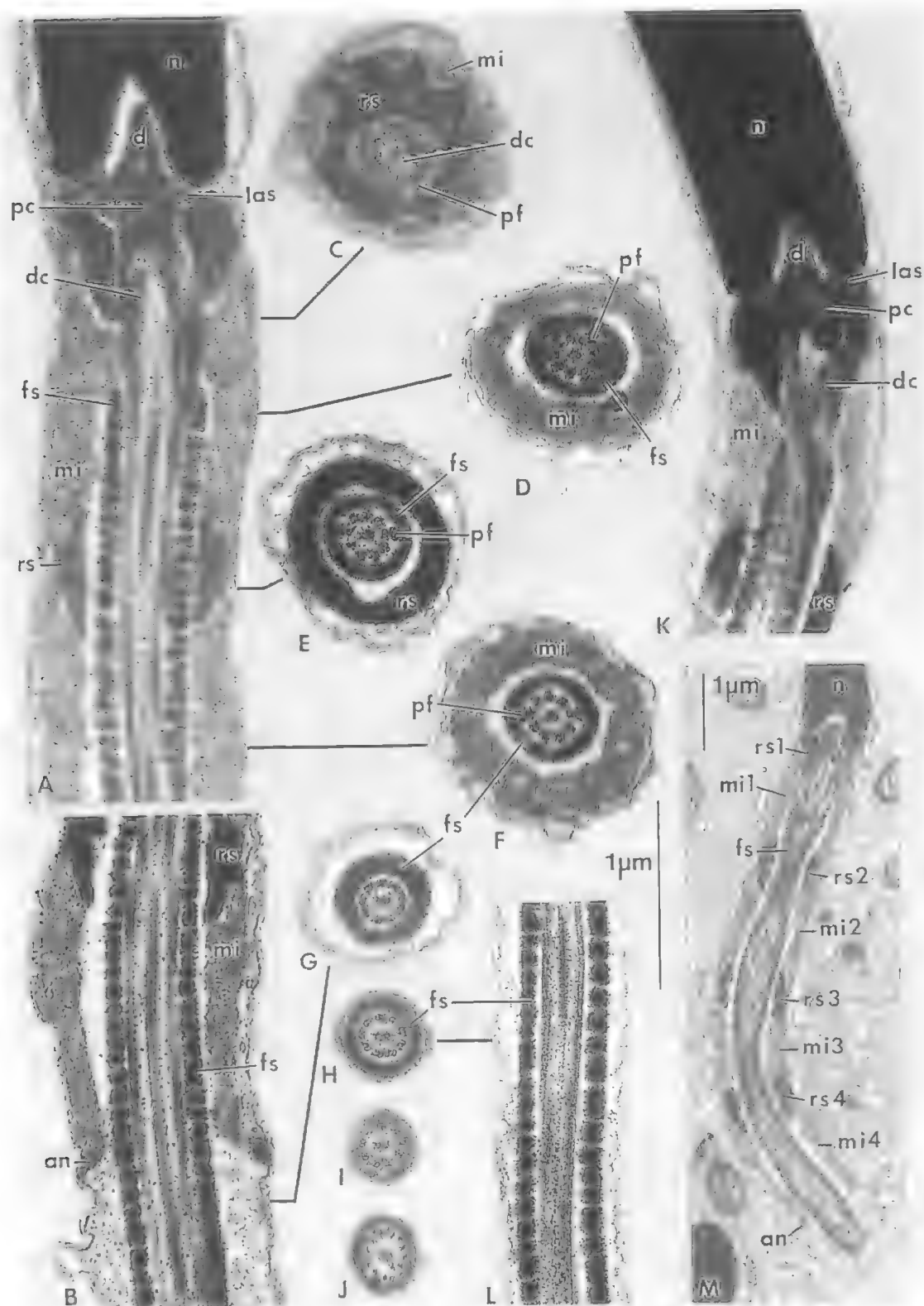
plane of curvature and elliptical in transverse section. The anterior region of the acrosome of *Tiliqua* becomes increasingly depressed and elliptical in transverse section. (Figs 1D-G; 5E-I; cf. *Carlia*, Figs 3E-J).

ACROSOME COMPLEX

The anterior end of the acrosome vesicle, comprising slightly less than half its total length, forms a thick walled hollow cone with a narrow lumen (subacrosomal space) housing the perforatorium (Figs 1C,D; 3C,E,G; 5B-F). The longer, posterior region of the vesicle is a thin walled continuation of this hollow cone, the vesicle here being no more than a sleeve-like investment (acrosome sleeve) of the subacrosomal material, as seen in longitudinal (Figs 1B,C,I; 3C; 5C) or transverse section (Figs 1E-G; 3H-J; 5G-I).

The perforatorium is a slender, moderately electron dense rod. In *Tiliqua* it shows some signs of internal longitudinal fibres (Fig. 5C). It extends anteriorly from the subacrosomal material, lying in the narrow subacrosomal space internal to the inner acrosome membrane (Figs 1C,D; 3C; 5B-D,F,K). In *Ctenotus* and *Tiliqua* the perforatorium extends through approximately the posterior half of the thick walled part of the acrosomal vesicle. A pale, central axial tube-like structure seen in *Ctenotus* (as in *Nangura spinosa*), which extends to the tip of the acrosome and displays some internal longitudinal fibres is not a forward continuation of the perforatorium. The perforatorium of *Carlia* extends from a perforatorial base plate (a pronounced basal swelling) to the apical tip of the acrosome (Fig. 3C). In all three species, the perforatorium makes contact at its posterior end with the subacrosomal material. Even allowing for the pronounced curvature of the acrosome of *Ctenotus* and *Tiliqua* the longitudinal axis of the perforatorium appears to be strongly oblique relative to that of the acrosome vesicle (Figs 1C; 5B,C) while that of *Carlia* is only very slightly oblique (Fig. 3C).

The material of the subacrosomal cone is paracrystalline, its matrix having fine obliquely longitudinal and less distinct transverse striations, indicating that it forms a fine lattice (Figs 1D,E,F,I; 3G,H; 5K). For most of its length, from its posterior end anteriorly, the subacrosomal cone invests the tapered anterior end of the nucleus (nuclear point). The nuclear point terminates within the anterior limit of the subacrosomal material at an epinuclear electron lucent region (Figs 1B; 3C,H; 5B). This region is



well defined in *Carlia* and to a lesser extent in *Ctenotus*, however in *Tiliqua* its presence is dubious.

In transverse sections of the acrosome vesicle anterior to the subacrosomal cone of *Ctenotus* and *Tiliqua* spermatozoa (Figs 1D; 5E,F), the vesicle is seen to have a concentric zonation which in sequence from the perforatorium outwards is: a narrow space around the perforatorium; a wide, dense, homogeneous zone; a narrow zone with radial striations; a thin, dense, homogeneous layer apposed to the plasma membrane. The narrow radially striated zone is not apparent in *Carlia*.

NUCLEUS

The nucleus is curved and tapers to a point within the basal region of the acrosome (acrosome sleeve). The transition from the tapered region (nuclear point) to the much longer cylindroid region is abrupt but the 'shoulders' seen in *Carlia* and many other reptile (and even *Ascapus*) sperm are represented only by a gentle curvature on each side in *Ctenotus* and *Tiliqua*. The length of the nucleus from the base of the acrosome vesicle to the base of the nucleus of *Ctenotus taeniolatus*, *Carlia pectoralis* and *T. scincoides* respectively is 6.8 μm , 2.9 μm and 5.1 μm with a further 2.8 μm , 0.96 μm and 1.9 μm for the nuclear point which is surrounded by the subacrosomal cone (Figs 1C,I; 3B,C; 5B,C). The nucleus is almost parallel-sided, showing only a slight increase in width posteriad, from 0.64 to 1.0 μm , 0.7 to 1.1 μm and 0.57 to 0.9 μm for *Ctenotus*, *Carlia* and *Tiliqua*, respectively, reaching its greatest width shortly before its posterior end. The cross section of the nucleus is circular throughout (Figs 1H; 3K; 5J; 6C). The chromatin is condensed and strongly electron dense. Basally the nucleus has a compact conical fossa which houses dense material extending from the proximal centriole (Figs 2A,K; 4A; 6A,K). The shape of the nuclear fossa varies from a dome shape in *Carlia* to a pointed cone in *Ctenotus*,

with *Tiliqua* intermediate between these two states.

NECK REGION

The neck region (Figs 2A,K; 3D; 4A; 6A,K) is the region where the nucleus joins the midpiece and is recognized by virtue of its internal components although the anterior end of the midpiece directly abuts the posterior end of the nucleus. The neck region includes the proximal and distal centrioles and associated densities, including the first of the dense structures (mitochondrial transformations) of the midpiece. Each centriole consists of 9 triplets. The proximal centriole lies immediately anterior to the distal centriole and with its long axis at slightly less than a right angle to it (Figs 2A,K; 4A; 6A).

The long axis of the distal centriole, which forms the basal body of the flagellum, is in the long axis of the axoneme. In *Ctenotus* and *Tiliqua* the centrioles do not lie in the basal nuclear fossa but the proximal centriole, immediately behind this, is surmounted by a hollow conical density (dense cone) which conforms in shape with the nuclear fossa which it occupies. An electron lucent space separates it from the wall of the fossa. Compact dense material extends from the base of the dense cone to cover the more axial end of the proximal centriole and insinuates itself as a large mass between the proximal and distal centrioles (Figs 2A,K; 4A; 6A,C). In *Carlia* (Fig 3D) the proximal centriole is surrounded by a narrow zone of dense material but there is no conical extension of this; the anterior portion of the centriole is situated in the wide and shallow nuclear fossa and is closely apposed to the nucleus. In all three species two central singlets of the axoneme extend anterior at least into the region of transition between the distal centriole and the axoneme. Unlike the proximal centriole, the distal centriole appears to always contain two central singlets, although longitudinal sections suggest that these are absent from its extreme anterior end. There is a density connecting triplet

FIG. 2. *Ctenotus taeniolatus*. A, longitudinal section (L.S.) through the neck region showing, as a squamate autapomorphy, that the fibrous sheath penetrates the midpiece almost to the junction between the axoneme and the distal centriole; B, L.S. through the midpiece-principal piece junction showing the annulus; C, L.S. through the distal centriole-axonemal transition showing the 9 peripheral fibres associated with the triplets or doublets; D, T.S. through the midpiece showing 9 peripheral fibres associated with the doublets; E, T.S. through a ring structure; F, T.S. through the midpiece showing 10 mitochondria surrounding the axoneme; G, H, T.S. through the principal piece; I, J, T.S. through the endpiece; K, L.S. through the neck region; L, L.S. through the principal piece; M, L.S. through the midpiece showing the four ring structures and annulus separated by four sets of columnar mitochondria. A-L to the same scale, as indicated. Abbreviations: an = annulus; d = dense cone; dc = distal centriole; fs = fibrous sheath; las = lamellar structure; mi = mitochondria; n = nucleus; nf = nuclear fossa; pc = proximal centriole; pf = peripheral fibre; pm = plasma membrane; rs = ring structure.

3 with the adjacent central singlet in addition to the peripheral dense fibre connected to each triplet or doublet (Figs 2C; 4C; 6E,F). The peripheral dense fibres are detached in some sections, indicating the commencement of the corresponding longitudinal column.

A conspicuous stratified laminar structure is seen in *Ctenotus* and *Tiliqua* to form a wing-like projection on each side of the proximal centriole near its anterior limit and is continuous around its axial pole (Figs 2A,K; 6A,D,K). It is therefore seen in some longitudinal profiles of the sperm, which are parallel to but not through the long axis of the axoneme, as a continuous wide lamina spanning much of the width of the nucleus behind the nuclear fossa (Fig. 6M). It is deduced that the lamina forms a thick disc around the proximal centriole but that the disc is interrupted at the peripheral end of the proximal centriole. Evidence for this interpretation is also seen in some transverse sections of the neck through the proximal centriole (Fig. 6M). In *Ctenotus* and *Tiliqua*, the outer edges of the laminar structure make contact with the first of the dense 'ring structures' of the midpiece, which are described below (Figs 2A,K; 6A,K) as does the peripheral end of the proximal centriole (Fig. 6D).

MIDPIECE

The midpiece includes the neck, described above. It consists of mitochondria, mitochondrial transformations (ring structures or dense bodies) and the contained axoneme with its fibrous sheath and ends posteriorly with the annulus.

In *Ctenotus* and *Tiliqua* the mitochondrial transformations are in the form of four ring structures (rs 1-4) in longitudinal succession, posterior to which lies the much smaller annulus. The ring

structures, with the annulus, are separated by mitochondrial regions (mi 1-4). In terms of the pattern recognised for the teiid lizard *Cnemidophorus* by Newton & Trauth (1992), the formula for *Ctenotus* and *Tiliqua* are rs1/mi1, rs2/mi2, rs3/mi3, rs4/mi4, an. Each ring structure appears in longitudinal section as an approximately kidney-shaped density on each side of the fibrous sheath of the axoneme (Figs 2A,M; 6A,B,M). In *T. scincoides*, as in *Nangura*, but less noticeably in *Ctenotus taeniolatus*, the profile of a ring structure on one side is often staggered relative to that on the other, though always overlapping it. This indicates that each ring structure is tilted relative to the axonemal axis (Figs 2A,M; 6A,B,M). In *Ctenotus taeniolatus* tilting is negligible. The mitochondrial transformations of *Carlia* are seen as scattered irregular dense bodies of varying sizes (Figs 3D; 4A-E,J).

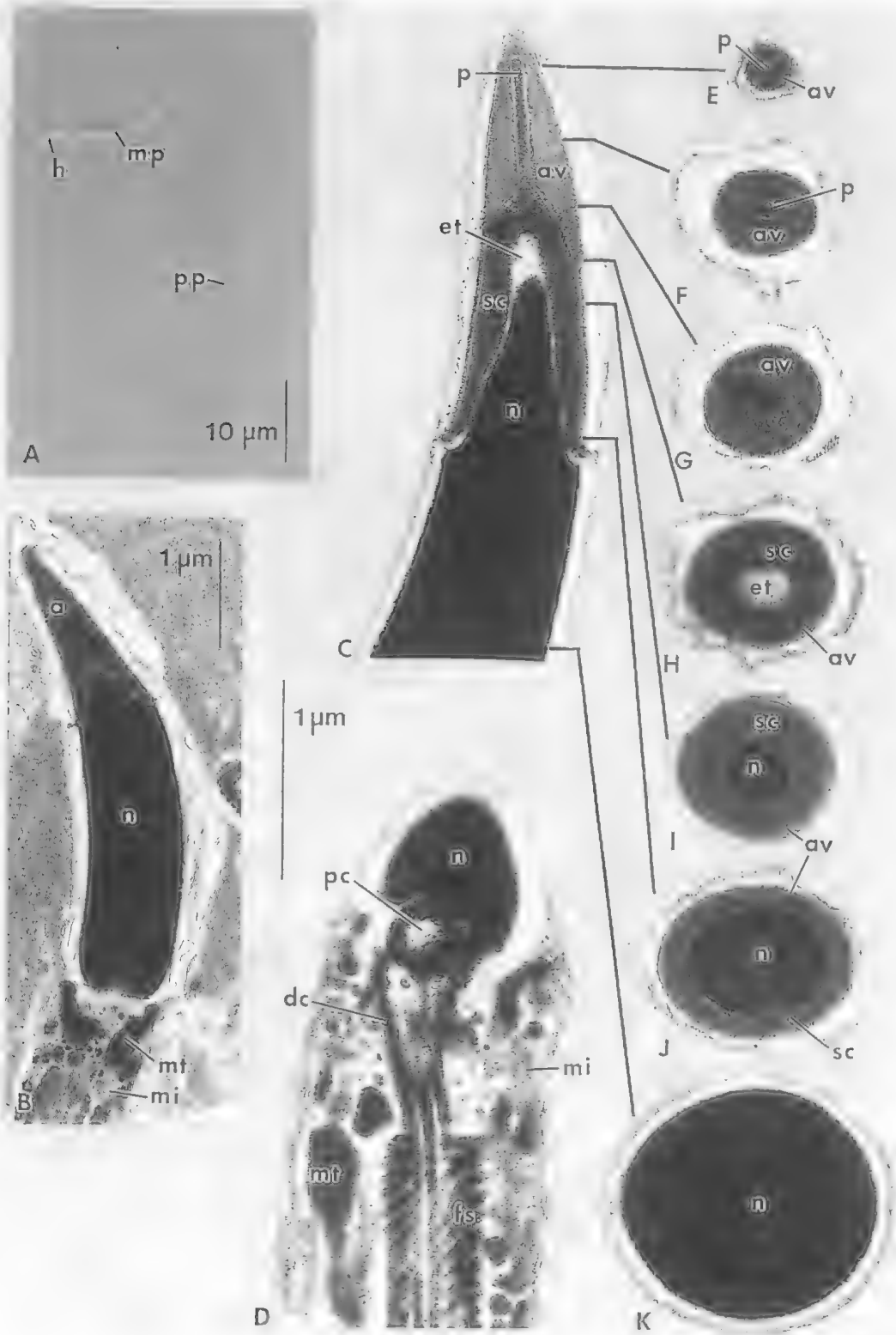
The mitochondria of *Ctenotus* and *Tiliqua* mostly form elongate, slightly sinuous columnar structures, with numerous predominantly longitudinal cristae, each of which extends from one ring structure to the next (Figs 2A,B,K,M; 6A,B,K,M). There are 10 or more (*Ctenotus*), or 9 or more (*Tiliqua*) mitochondria around the axoneme as seen in transverse section (Figs 2F; 6I). Occasional single, ovoid mitochondria are seen. Small mitochondria are often present lateral to the ring structures, the outer surface of which is then scalloped by them (Figs 2C; 6G).

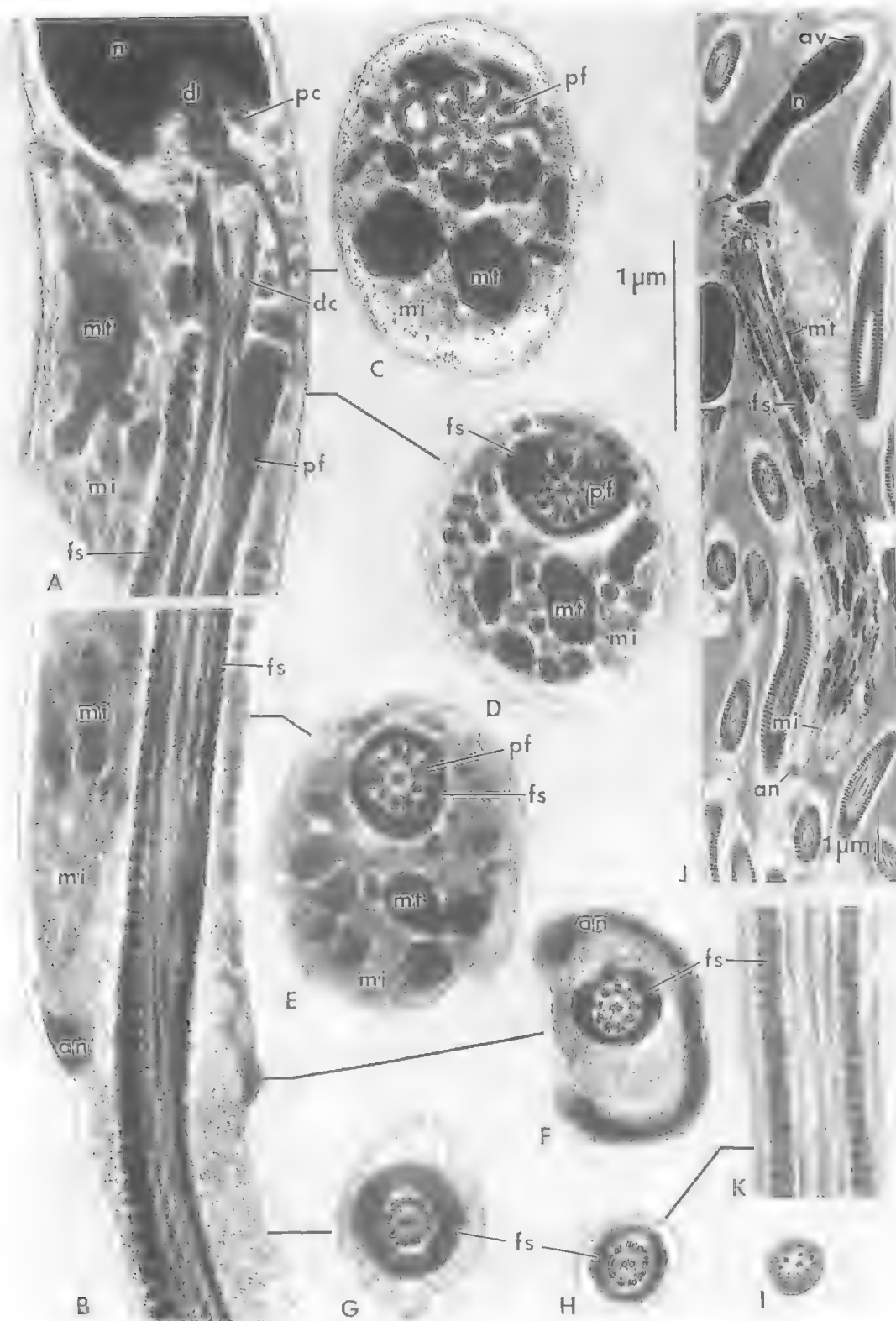
The mitochondria of *Carlia* are elongate, tubular structures, with longitudinal cristae, which weave between the intermitochondrial bodies (Fig. 4A-E, J). In transverse section more than 25 mitochondria can usually be seen (Fig. 4E).

The axoneme has the usual pattern of nine doublet and two central singlet microtubules.

FIG. 3. *Carlia pectoralis*. A, whole spermatozoon (Nomarski contrast light microscopy). B, L.S through the nucleus; C, L.S through the acrosome showing the nuclear point, distinct nuclear 'shoulders', and acrosome; D, L.S through the neck region; E-J, a series of transverse sections (T.S) through the acrosome; K, T.S through the nucleus; C-K to the same scale, as indicated. Abbreviations: a = acrosome; av = acrosome vesicle; et = epinuclear electron lucent region; mp = midpiece; n = nucleus; p = perforatorium; pb = base plate of perforatorium; pm = plasma membrane; pp = principal piece; sc = subacrosomal cone; sh = nuclear 'shoulders'.

FIG. 4. *Carlia pectoralis*. A, longitudinal section (L.S) through the neck region showing that the fibrous sheath penetrates the midpiece almost to the junction between the axoneme and the distal centriole; B, L.S through the midpiece-principal piece junction showing the annulus; C, T.S through the distal centriole-axonemal transition showing the 9 peripheral fibres associated with the triplets or doublets; D, T.S through the midpiece showing the enlarged peripheral fibres at doublets 3 and 8; E, T.S through the midpiece showing the intermitochondrial bodies and mitochondria; F, Oblique T.S through the annulus; G, H, T.S through the principal piece; I, T.S through the endpiece; J, L.S through the length of the midpiece; K, L.S through the principal piece. A-I and K to the same scale, as indicated. Abbreviations: an = annulus; d = dense cone; dc = distal centriole; fs = fibrous sheath; las = laminar structure; mi = mitochondria; n = nucleus; nl = nuclear fossa; pc = proximal centriole; pf = peripheral fibre; pm = plasma membrane; rs = ring structure.





Each doublet has two dynein arms. The A sub-tubule is occluded by dense material. Around the axoneme almost as far anteriorly as its junction with the distal centriole, there is a fibrous sheath (Figs 2A,K,M; 3D; 4A; 6A,K,M). In longitudinal section (Figs 2A,L; 4K; 6B,L) the fibrous sheath exhibits regularly arranged, approximately square to oblong dense blocks which, from glancing longitudinal sections (Figs 2M; 4J; 6M) and transverse sections (Figs 2D-H; 4D-H; 6G-J) are shown to form rings around the axoneme. They show a tendency to tilt relative to the axonemal axis and there are interruptions in the cross sections but that they form a spiral is questionable. Occasional anastomoses of adjacent rings are seen in tangential longitudinal sections.

Nine large peripheral dense fibres are associated with the transition between the distal centriole and the axoneme (Figs 2C-D; 4C-D; 6E-F) and continue posteriorly, though much narrower, along the axoneme into the midpiece (Figs 2E-F; 4E; 6G-I). One is attached externally to each triplet or doublet. Within the midpiece, at an undetermined level, all but two of the peripheral fibres become greatly reduced in size. Only peripheral fibres adjacent to doublets 3 and 8 remain conspicuous, as a double structure which for most of its length is nearer the fibrous sheath than it is to its doublet (Figs 2F; 6I). At the anterior end of the fibrous sheath in *Carlia* the peripheral fibres adjacent to doublets 3 and 8 are greatly enlarged, for a short distance, compared to *Ctenotus* and *Tiliqua* (Figs 2D; 4D; 6G). Peripheral fibres are seen in longitudinal section to be cross striated (Fig. 6A). In all three species,

as in *Nangura spinosa*, the only well developed, though small, peripheral fibres at the level of the annulus are the double fibres at doublets 3 and 8 (Fig. 4F); at the beginning of the principal piece all nine dense fibres are already vestigial or absent (Figs 2G; 4G); and they are absent from the remainder of the principal piece (Figs 2H; 4H; 6J).

The annulus (Figs 2B,M; 4B,F,J; 6B,M) is a small dense ring with an irregular oval cross section. It is closely applied to the inner surface of the plasma membrane.

PRINCIPAL PIECE

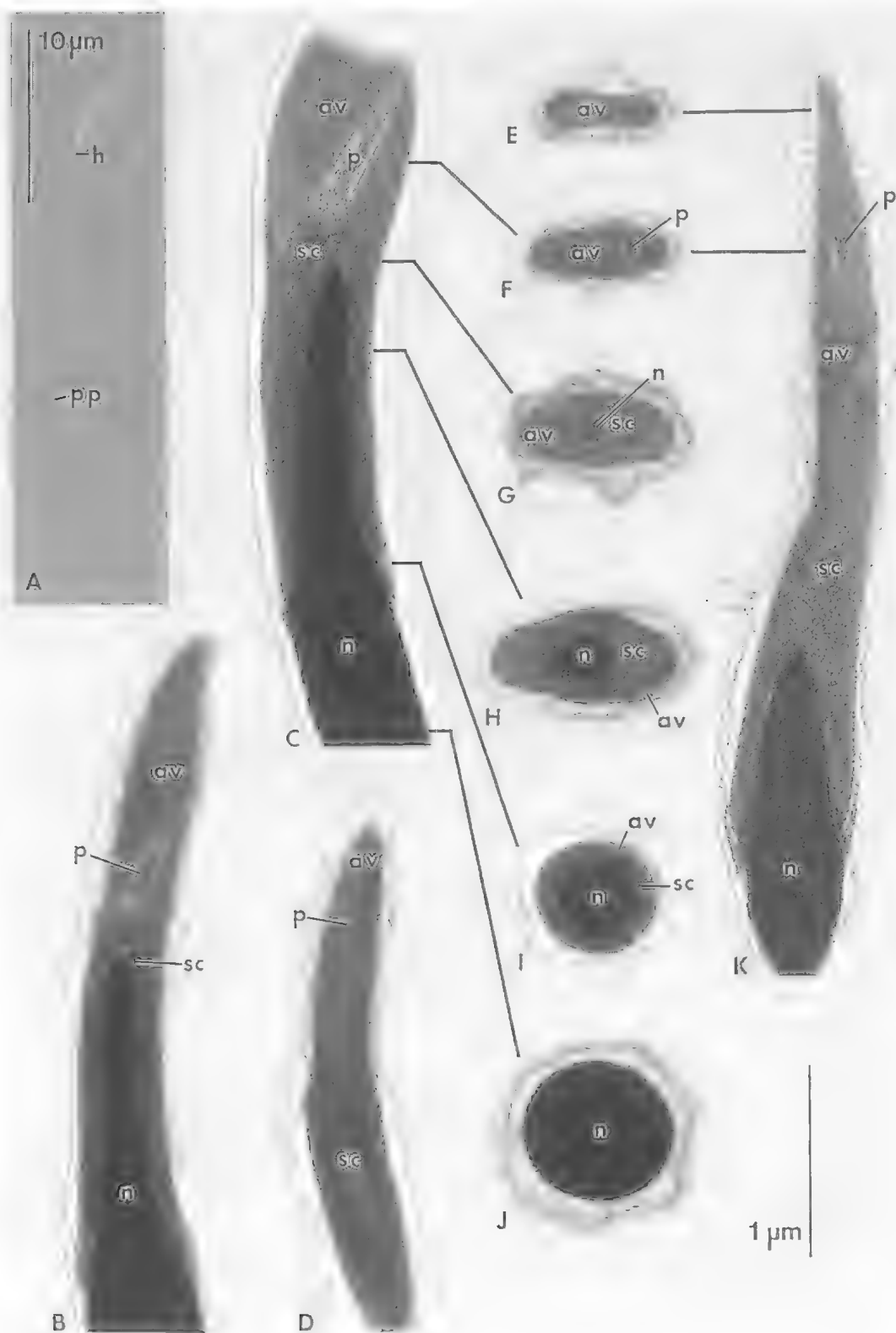
The principal piece, the longest part of the spermatozoon, consists of the continuation, behind the midpiece, of the axoneme with its surrounding fibrous sheath and plasma membrane. It begins, immediately behind the annulus, with a short region in which a wide zone of cytoplasm intervenes between the fibrous sheath and the plasma membrane (Figs 2B,G; 4B,G; 6B). The cytoplasm is finely granular, giving the region some resemblance to a glycogen piece but the presence of glycogen has not been determined. Posterior to this the plasma membrane is closely approximated to the fibrous sheath (Figs 2H,L; 4H,K; 6J,L).

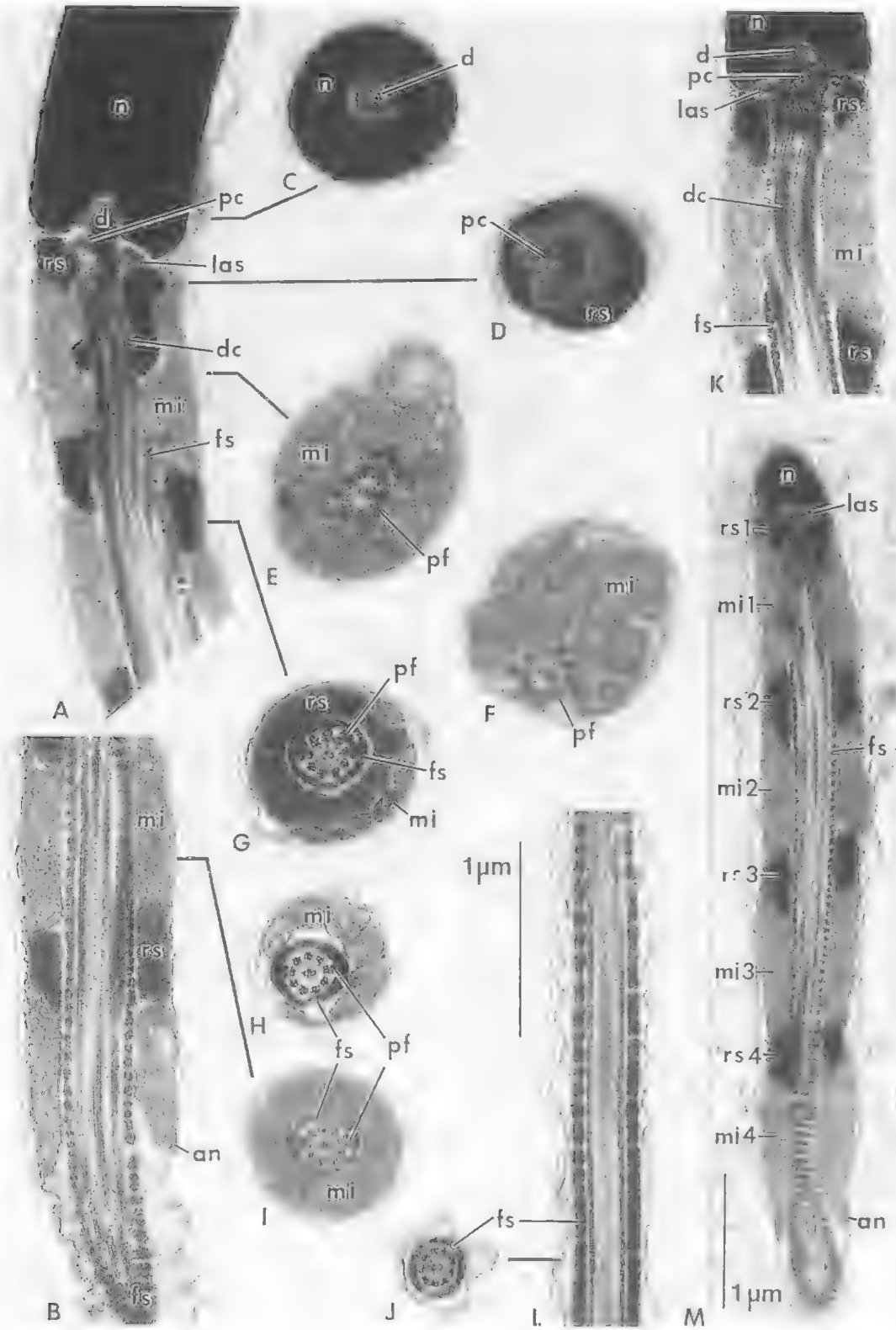
ENDPIECE

The axoneme projects behind the fibrous sheath as an endpiece of undetermined length (Figs 2I-J; 6I). Within it the arrangement of microtubules becomes disrupted (Fig. 4I).

FIG. 5. *Tiliqua scincoides scincoides*. A, whole spermatozoon (Nomarski contrast light microscopy); B, L.S. through the nuclear point; C, L.S. through the acrosome showing the nuclear point and that the longitudinal axis of the perforatorium appears to be slightly oblique relative to that of the acrosome vesicle; D, L.S. through the perforatorium; E-I, a series of transverse sections (T.S.) through the acrosome. (Note that anteriorly, in E-H, the acrosome is depressed in transverse sections, while at its posterior limit, in I, it is circular); J, T.S. through the nucleus; K, L.S. through the length of the acrosome. B-K to the same scale, as indicated. Abbreviations. a = acrosome; av = acrosome vesicle; et = epinuclear electron lucent region; mp = midpiece; n = nucleus; p = perforatorium; pm = plasma membrane; pp = principal piece; sc = subacrosomal cone.

FIG. 6. *Tiliqua scincoides scincoides*. A, longitudinal section (L.S.) through the neck region showing, that the fibrous sheath penetrates the midpiece almost to the junction between the axoneme and the distal centriole; B, L.S. through the midpiece-principal piece junction showing the annulus; C, T.S. through the nuclear fossa; D, L.S. through the proximal centriole; E, F, T.S. through the distal centriole-axonemal transition showing the 9 peripheral fibres associated with the triplets or doublets; G, T.S. through a ring structure; H, T.S. through the midpiece showing that the mitochondria may not completely surround the axoneme; I, T.S. through the midpiece showing 9 mitochondria surrounding the axoneme; J, T.S. through the principal piece; K, L.S. through the neck region showing the proximal centriole in transverse section; L, L.S. through the principal piece; M, L.S. through the midpiece showing the four ring structures and annulus separated by four sets of columnar mitochondria. A-L to the same scale, as indicated. Abbreviations. an = annulus; d = dense cone; de = distal centriole; fs = fibrous sheath; las = laminar structure; mi = mitochondria; n = nucleus; nf = nuclear fossa; pc = proximal centriole; pf = peripheral fibre; pm = plasma membrane; rs = ring structure.





DISCUSSION

Extension of the fibrous sheath into the mid-piece seen in the sperm of the three species examined is an autapomorphy of the Squamata, unknown in the sperm of other reptiles or other amniotes (Healy & Jamieson, 1992; Jamieson & Healy, 1992).

Ctenotus taeniolatus is placed by Greer (1979) in the *Sphenomorphus* group. The sperm of *Nangura spinosa*, *Ctenotus robustus* and *Anomalopus verreauxii*, which are also in the *Sphenomorphus* group, have been examined by Jamieson & Scheltinga (1993; unpubl. data). *Carlia pectoralis* is included in the *Eugongylus* group of Greer (1979). Jamieson et al. (unpubl.) have examined the sperm of *Cryptoblepharus virgatus*, in the *Eugongylus* subgroup, and *Lampropholis delicata*, in the *Lampropholis* subgroup (this subgroup also includes *Carlia*). Greer's third group, the *Egernia* group, includes *Tiliqua scincoides scincoides*.

The species of the *Sphenomorphus* and *Egernia* groups are more similar to each other than they are to the *Eugongylus* group in possessing an anteriorly depressed acrosome and a sequence of ring structures in the midpiece. The species of the *Eugongylus* group differ in having scattered intermitochondrial bodies (considered homologous with the ring structures) in the form of small dense irregular spheres, tortuous rods or large plates and a shorter acrosome which is circular in transverse section.

The sperm of *Chalcides ocellatus tiligugu* examined by Furieri (1970) resemble *Ctenotus* and *Tiliqua* in having four regularly placed intermitochondrial rings but, unlike *Ctenotus* and *Tiliqua*, each ring is shown in a diagram, unsubstantiated by micrographs of transverse sections, to consist of a circlet of small juxtaposed spherules rather than a continuous ring. *Varanus gouldii flavirufus* also has 4 dense intermitochondrial structures in longitudinal sequence. However, each 'ring' is made of many loosely aggregated large granules that do not form a continuous ring (Oliver & Jamieson, unpublished). The sperm of the Lacertidae examined by Furieri (1970) also have intermitochondrial rings but only two are present, one around the proximal centriole, the other in the distal third of the midpiece.

A paracrystalline substructure of the sub-acrosomal cone, as here seen in skinks, has been recognized in other squamates (Butler & Gabri, 1984; Carcupino et al., 1989; Furieri, 1970). It is

probably (Jamieson & Scheltinga, 1993) a synapomorphy, and autapomorphy, of the Squamata.

A dense ring, the annulus, at the posterior end of the midpiece is a feature of many metazoan sperm and is clearly plesiomorphic for amniotes. It has been demonstrated, inter alia, in turtles, crocodile, tinamou, Rhea, rooster, guineafowl, tuatara and monotremes. Squamates were considered exceptional in absence or at least negligible development of an annulus (Jamieson & Healy, 1992). However, an annulus has been demonstrated for *Lacerta vivipara* (see Courten & Depeiges, 1985), *Cnemidophorus sexlineatus* (see Newton & Trauth, 1992) and for *Nangura spinosa* (see Jamieson & Scheltinga, 1993) and is possibly universal in squamates and, indeed, in reptiles, despite supposed absence in some accounts.

The number of mitochondria seen in transverse section of the midpiece, where possible near its anterior end, is very variable in amniotes. The number, approximately, 10 in *Ctenotus*, 9 in *Tiliqua* and 25 or more in *Carlia* is apomorphically high.

The intermitochondrial bodies, seen as 'ring structures' in *Ctenotus*, *Tiliqua* and *Nangura*, or irregular scattered dense bodies in *Carlia*, are limited to the squamates and were regarded as derivations of the dense bodies seen in basic amniotes (Jamieson & Healy, 1992). This derivation has received ontogenetic confirmation in the spermiogenesis of some squamates (Oliver & Jamieson, unpubl. data; Jamieson & Scheltinga, 1993). Carcupino et al. (1989), for *Chalcides ocellatus tiligugu*, independently concluded that the rings were mitochondrial derivatives.

ACKNOWLEDGEMENTS

Mrs. Lina Daddow and Ms. G. Gosper are thanked for excellent technical assistance. This work was made possible by an ARC small grant.

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NEW DATA ON *SALTUARIUS OCCULTUS*, A RECENTLY DESCRIBED, POORLY KNOWN LEAF-TAILED GECKO. *Memoirs of the Queensland Museum* 37(1):194, 1994:- *Saltuarius occultus* Couper et al., 1993 is known only from its type locality, McIlwraith Ra. (13°45'S 143°19'E), FNQ, an area of upland notophyl vine forest on granite. Specimens on which its description was based were collected in 1979, and the species has not been observed since. As the four type specimens have regenerated tails, the original tail of this species has not been described.

In May 1994, we visited the type locality to observe and photograph *S. occultus*. The site investigated is on Peach Ck (13°46'S 143°20'E, alt 560±30m) where weathering has left large granite boulders piled along the creek bed. There is a sharp transition in the creek bed from sand to boulders at an altitude of approximately 500m. These boulders are smooth and covered in mosses, lichens and ferns. Their bare, shaded undersides are weathered into a mass of cracks and crevices.

On May 26, while spotlighting, we found two specimens of *S. occultus* on the underside of these boulders. Many specimens of *Cyrtodactylus lousiadensis* were observed on the exposed boulder faces at the same time. One of the *S. occultus* specimens we observed had an original tail (Fig.1). This had an attenuated tip, a dorsal surface of small rounded

tubercles in longitudinal rows, and flanged edges surrounded by clusters of two to three sharply pointed tubercles which diminish in size posteriorly. The colour description of this species was based only on spirit material (Couper et al., 1993). In life, the original tail of *S. occultus* is darker than as described (Couper et al., 1993). It bears light blotches similar to those on the body.

Acknowledgements

Dr John Winter provided advice about collection localities. Jeanette Covacevich and Patrick Couper, Queensland Museum, commented constructively on this note.

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P.J. Lethbridge, T.A. Hawkes, M. Anthony & M. McGregor, Cape York Herpetological Society, PO Box 114, Palm Cove (Cairns), Queensland 4879, Australia; 30 September 1994.

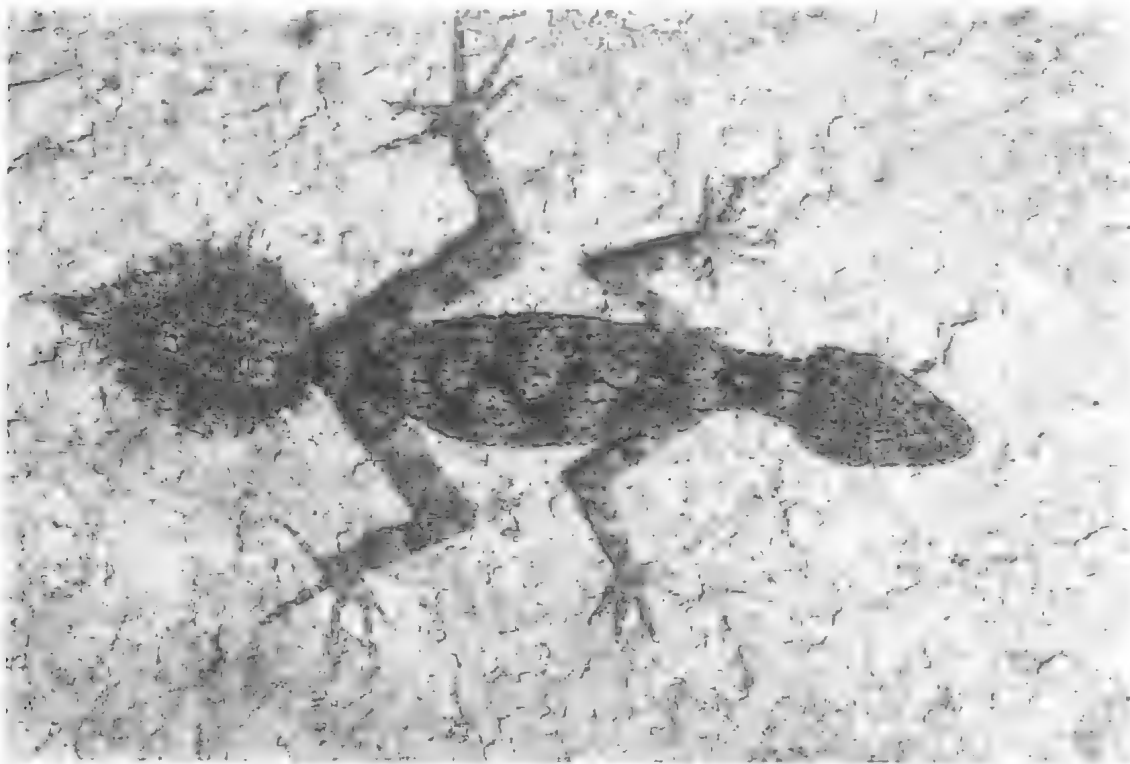


FIG. 1. The first photograph of *Saltuarius occultus* in life, showing original tail. (P. Lethbridge).

THE LOGGERHEAD TURTLE, *CARETTA CARETTA*, IN QUEENSLAND: POPULATION STRUCTURE IN A WARM TEMPERATE FEEDING AREA.

COLIN J. LIMPUS, PATRICK J. COUPER AND MARK A. READ

Limpus, C.J., Couper, P.J. & Read, M.A. 1994 12 01: The Loggerhead Turtle, *Caretta caretta*, in Queensland: population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum* 37 (1):195-204. Brisbane. ISSN 0079-8835.

Caretta caretta, resident in the Moreton Banks within eastern Moreton Bay, southeastern Queensland, encompass all size classes from immature turtles with a curved carapace length of 70.1cm to mature adults of both sexes. The population is strongly biased to males (64.8%) and to immature size classes (72.6% of males, 62.1% of females). Sexual maturity does not usually occur at the minimum size for the breeding population but at some larger size. Tag recoveries indicate that most of the adult females resident in this feeding area migrate to breed at the mainland rookeries of the Bundaberg coast. Approximately 11% of the population show signs of anthropogenic impacts and/or health problems which range from fibropapillomas to propeller damage. □ *Caretta*, Moreton Bay, feeding area, population structure, sex ratio, sexual maturity, migration.

C.J. Limpus, Queensland Department of Environment and Heritage, P.O. Box 155, Brisbane, Queensland 4002, Australia; P.J. Couper, Queensland Museum, P.O. Box 3300, South Brisbane, Queensland 4101, Australia; M.A. Read, Department of Zoology, University of Queensland, St. Lucia, Queensland 4072, Australia; 1 June 1994.

The decline in nesting populations of the Loggerhead Turtle, *Caretta caretta* in eastern Australia is the result of mortality of the turtles in their feeding areas (Limpus and Reimer, 1994). While there is considerable knowledge of the breeding biology of *C. caretta* from nesting beach studies, reproduction occupies a small portion of their life history. Most of their life is spent at sea where the biological understanding of them is scant (Dodd, 1988). Concern for the survival of this species in Australia is reflected in *C. caretta* being listed as endangered under the Australian Endangered Species Act, 1992. To improve our understanding of the species in its feeding grounds, the present study was undertaken on a large assemblage of *C. caretta* resident in Moreton Bay.

METHODS

The present study was done in conjunction with another of *Chelonia mydas* in the same habitats (Limpus et al., 1994). Turtles were captured using the turtle rodeo capture method (Limpus & Reed, 1985) over the intertidal flats and adjacent margins of the Moreton Banks and the Maroom Banks between July 1990 to June 1992. Each turtle was tagged with one or more tags applied in the front flipper axillary tagging positions (Limpus, 1992a). The tags used were either large size, 125 CPT titanium turtle tags (Stockbrands Pty. Ltd., Perth, Western Australia) or inconel

625 turtle tags (National Band and Tag Co. New Port, Kentucky).

Curved carapace measurements were taken using a flexible fibreglass tape measure (± 0.1 cm) extended over the curve of the carapace. These measurements are the standard measurements used for *C. caretta* in eastern Australia (Bustard, 1972; Limpus, 1985; Limpus et al., 1984). The calibration of fibreglass tape measures was checked regularly against steel rules and a tape measure was rejected for use when length changes exceeded 0.2%. Large barnacles on the carapace likely to interfere with a measurement were removed. Curved carapace length (CCL) was measured along the midline from the junction of the skin and carapace above the neck to the posterior margin of the carapace at the midline junction of the supracaudal scutes. Tails were measured (TLC, ± 0.5 cm) with either a steel or a fibreglass tape measure from the posterior edge of the midline junction of the supracaudal scutes to the tip of the extended, straightened tail. A negative sign for this measurement indicates a distance short of the carapace margin. Turtles were weighed using 100 or 200kg Salter spring balances (± 0.5 , ± 1.0 kg respectively). All turtles were measured for CCL except those with damage to the posterior carapace. An unbiased series of turtles were weighed and TLC measured. Each turtle within this two year study was analysed for only one set of measurements, usually those taken at the time of first capture.

TABLE 1. Frequency distribution of 51 recoveries of tagged adult female *Caretta caretta* from Moreton Bay and adjacent waters which were previously tagged while nesting at rookeries in the southern Great Barrier Reef and adjacent mainland (Limpus et al., 1992 and unpublished records of the Queensland Turtle Research Project). These data include 11 recaptures of migrant females from the Moreton Banks of the present study.

| Rookery of origin | Present study | Reported by the public | | |
|-------------------|---------------|------------------------|-----------------|-------------|
| | | trawled | | non-trawled |
| | | inside Moreton Bay | adjacent waters | |
| Mon Repos | 6 | 19 | 3 | 6 |
| Wreck Rock | 2 | 3 | 2 | 3 |
| Heron Is. | 1 | | | 1 |
| Wreck Is. | 2 | 2 | | |
| Tryon Is. | | | 1 | |
| Total | 11 | 24 | 6 | 10 |

The number of turtle barnacles, *Chelonibia testudinaria*, with diameter greater than 1 cm on the carapace were counted. When the recapture interval exceeded a year, a recount of these barnacles was included in the analysis.

The gonads and associated reproductive ducts were examined using laparoscopy to assess sex, maturity and reproductive status of the turtle (Limpus & Reed, 1985). The size and morphology of the reproductive organs were used to assess sex, maturity and breeding status after methods described for *C. mydas* (Limpus & Reed, 1985), *C. caretta* (Limpus, 1985) and hawksbill turtles, *Eretmochelys imbricata* (Limpus, 1992b). Immature turtles were identified by incompletely developed gonads and associated ducts. In small immature females the oviduct was always straight and the stroma of the ovary non expanded. In small immature males the epididymis was contained within the body wall and the testis extremely ovoid in cross-section. Pubescent immature turtles were identified by the criteria of Limpus (1992b): females had a partly convoluted oviduct that was 0.3-1.5 cm in diameter and oval in cross-section; males had a non-pendulous epididymis bulging from the body wall. For those turtles whose sex was not determined via laparoscopy, the sex of some males was determined using tail length (Limpus, 1985: adult male when TLC was greater than 19 cm; immature male when TLC was greater than 5 cm and less than 19 cm). For the remainder, if TLC

was less than 5 cm the turtle was scored as unsexed; if CCL was less than 80 cm the maturity status was scored as immature (CCL = 80 cm is the size of the smallest recorded breeding adult female at the southern Great Barrier Reef [GBR] rookeries: Limpus, 1985; Limpus et al., 1984). The year of breeding for an adult female was determined as follows: breeding in the current breeding season if she was observed on a nesting beach or if she was in advanced vitellogenesis in the months preceding a breeding season; bred in the previous breeding season if she had healing corpora lutea (corpora albucantia) greater than 3 mm in diameter during the months following a breeding season; bred in the penultimate breeding season if she had corpora albucantia approximately 3 mm in diameter.

Some turtles were recaptured from two prior studies outside of Moreton Bay:

1. *Nesting studies.* Thousands of nesting female *C. caretta* have been tagged on nesting beaches along mainland south Queensland since 1968 and in the southern GBR since 1977 (Limpus et al., 1992). Between 1977 and 1992, comparable numbers of nesting females have been tagged annually in the two major *C. caretta* rookery regions of eastern Australia: 4304 within the Capricorn-Bunker Groups of the southern GBR; 4495 along the mainland coast from Bundaberg to Bustard Head.

2. *Hatchling marking studies.* During the period January 1976 - March 1983, 129921 hatchling *C. caretta* were marked by mutilation tagging at Mon Repos and Heron Island. These turtles can be identified to year and rookery of

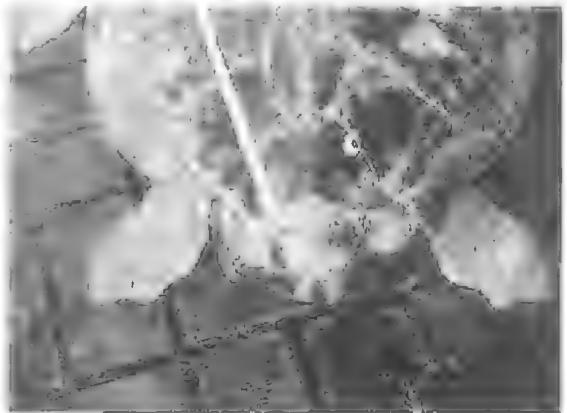


FIG. 1. Subadult female *Caretta caretta* (tag number T56404) marked as a hatchling at Mon Repos and recaptured on the Moreton Banks at 15.2 years of age. See text for details.

birth by the distinctive pattern of damage to a pair of marginal scutes (one scute on either side of the posterior carapace with symmetrically placed damage within each scute. An arbitrary birth date of 1 February was assigned to these marked hatchlings within each breeding season (Limpus, 1985).

Original capture data for these turtles were obtained from the unpublished records of the Queensland Turtle Research Project.

STUDY SITE

The principal study site was the intertidal and subtidal sand flats of the Moreton Banks (27°21'S, 153°24'E) and adjacent Maroom Banks in eastern Moreton Bay, southeastern Queensland (Limpus et al., 1994). This study also summarised the climate, tidal range, salinity, substrate and vegetation of the area.

To identify capture sites within the Moreton Banks, the banks were divided into sectors which were defined by the boundaries of the low tide drainage areas (Anon, 1987). There were two inner drainage sectors, Day's Gutter and Brown's Gutter. There were three outer drainage sectors: Boorong Bank; Fisherman's Gutter; and the western margin of the Moreton Banks from Fisherman's Gutter to Blue Pool.

RESULTS

During the study, a total of 447 captures were made of 320 individual *C. caretta*: 434 captures of 308 turtles on the Moreton Banks and 13 captures of 12 turtles on the adjacent Maroom Banks. All except nine were released at the bank on which they were captured. Eight individuals were removed to other locations within Moreton Bay: 6 removed from Moreton Banks (two immature turtles to Peel Island [15km], two immature females to Raby Bay [20km], one adult female and one immature female to Maroom Banks [9.5km]); 1 immature female was removed from Maroom Banks and released on Moreton Banks; 1 injured immature male from the Moreton Banks was sent to Sea World for rehabilitation and subsequently released adjacent to the point of capture 30 weeks later. One immature male died during the research observations.

Most turtles were captured on the same bank on successive captures. Indeed, most were recaptured in the same drainage sector. Two turtles were recorded moving across the major channel (Rous Channel) between the Moreton and Maroom Banks. Four of the six turtles relocated

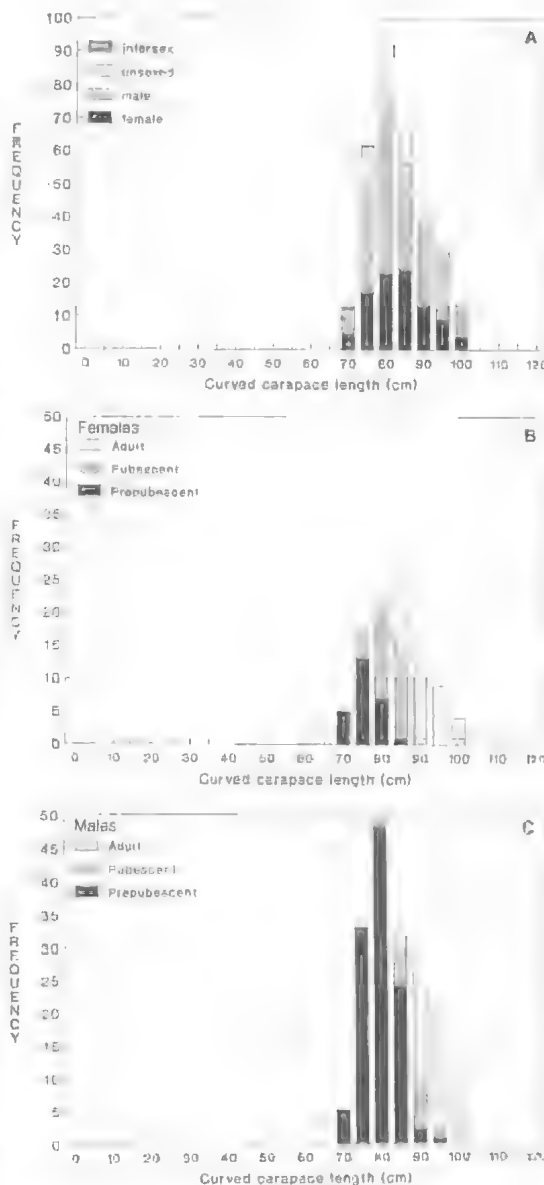


FIG. 2. Frequency distribution of size classes of *Caretta caretta* captured on the Moreton and Maroom Banks of Moreton Bay, August 1990 - June 1992. A, sex of individuals (n = 320); B, maturity status of females (n = 95); C, maturity status of males (n = 175). * denotes size of hatchling (Limpus, 1985).

to other sites from the Moreton Banks were subsequently recaptured back on the Moreton Banks: 2 from Peel Island; 1 from Raby Bay; the turtle rehabilitated at Sea World and released back at the Moreton Banks was recaptured still on the Moreton Banks 23 weeks post release. There

TABLE 2. Frequency distribution by size class, sex and maturity status for *Caretta caretta* captured on the Moreton and Maroom Banks.

| Sex | Maturity status | | | | Total |
|----------|-----------------|-----------|---------------------------|-------|-------|
| | Adults | Immature | | | |
| | | Pubescent | Pre-pubescent (CCL cm) | | |
| | | | >80.0 | <80.0 | |
| Male | 48 | 14 | 75 | 38 | 175 |
| Female | 36 | 33 | 8 | 18 | 95 |
| Intersex | | | | 2 | 2 |
| Total | 84 | 47 | 83 | 58 | 272* |

* There were an additional 48 unsexed turtles of which 13 with CCL <80.0cm were judged to be immature and 35 with CCL >80.0cm were of uncertain maturity.

were 71 instances of consecutive captures of turtles on the Moreton Banks for which the drainage sector was recorded for each capture: in 55 cases the turtle was recaptured within the same drainage sector; in 5 cases the turtle moved between adjacent outer drainage sectors; in 4 cases the turtle moved between non adjacent outer drainage sectors; and in 7 cases the turtle moved between inner and outer drainage areas. No turtle was recorded moving between adjacent inner drainage sectors. There was no significant difference in the size of turtles captured in the various drainage sectors (One way ANOV: $F = 0.87$; $df = 4,305$; $p > 0.5$).

Of the 320 turtles examined in this study, only 12 were recaptures of turtles that had been tagged elsewhere: 11 from nesting studies and 1 from hatchling marking studies. The eleven recaptures from nesting studies were of females tagged at Mon Repos and Wreck Rock on the mainland coast and Wreck and Heron Islands in the Capricorn Group, southern GBR, 402–480km to the north of Moreton Bay (Table 1). In addition, there have been 40 recaptures of tagged female *C. caretta* from elsewhere in Moreton Bay ($n = 34$) and adjacent waters ($n = 6$) that have also originated from distant nesting studies (Table 1). All of these adult female migrant recaptures were from two rookery regions, the southern GBR and the adjacent mainland near Bundaberg. The turtles had migrated from 286km up to 509km between their respective rookeries and the feeding area recapture sites. Considering only those females tagged from 1977 onwards, (the period during which nesting turtles were tagged in both rookery regions), the ratio of recaptures from each of these rookery regions (33:7) is sig-

nificantly different from the ratio of the number of nesting female *C. caretta* tagged at each of these rookery regions ($\chi^2 = 15.73$, $df=1$, $p < 0.0001$). This suggests that a female *C. caretta* resident in Moreton Bay is more likely to nest at a mainland rookery than at a coral cay rookery of the southern GBR.

Of the eleven adult females that had been tagged while at a distant rookery prior to their having been recorded on the Moreton Banks, two have been subsequently recorded nesting in a following breeding season back at their original rookery (X22706 Wreck Rock rookery, 5yr remigration interval; T41196 Mon Repos rookery, 3yr remigration interval). Both have subsequently completed their post-nesting migrations and been recorded again on the Moreton Banks.

One immature female (T56404; captured 19 April 1992 on the Moreton Banks, CCL = 75.6cm, Fig. 1) was consistent with having been marked by mutilation tagging when it was a hatchling at the Mon Repos rookery in Jan-Feb 1977. This immature female *C. caretta* was estimated to be 15.2yr old when captured on the Moreton Banks.

No recaptures were made during this study of *C. caretta* that had been tagged at other feeding areas in Queensland (Limpus, 1985). However, outside of this study period there has been a single recapture of a *C. caretta* in Moreton Bay from another study site (tag number 5020; tagged when captured in a shark net off Billunga, Gold Coast, south east Queensland, 10 February 1971; trawled in 'Moreton Bay', 10 November 1971. Not measured, not sexed.). Except for adult females that have been subsequently recaptured

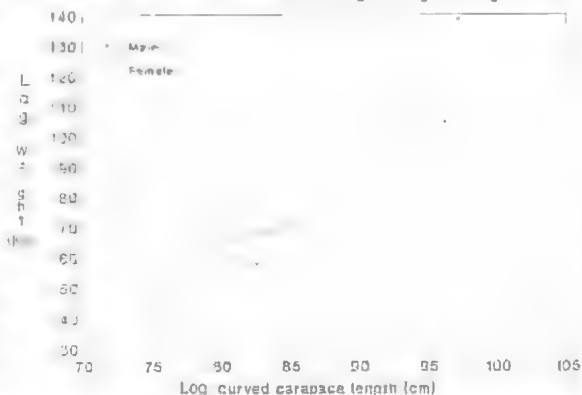


FIG. 3. Scatter plot of log carapace length (CCL) against log weight (Wt) for *Caretta caretta* captured on the Moreton Banks of Moreton Bay ($n = 48$).

TABLE 3. Results of stepwise unweighted logistic regression of sex ratio by size and maturity of *Caretta caretta* resident on the Moreton and Maroon Banks.

| Model | Deviance | d.f. | Log-likelihood ratio | | | |
|---------------------|----------|------|----------------------|-------|------|------------|
| | | | Source | LR | d.f. | p |
| S+A+Pu+Pr+SxA+SxPu* | 12.33 | 11 | | | | |
| S+A+Pu+Pr+SxA | 12.73 | 12 | SxPu | 1.0 | 1 | 0.25>p>0.5 |
| S+A+Pu+Pr | 13.76 | 13 | SxA | 2.06 | 1 | 0.25>p>0.1 |
| A+Pu+Pr | 50.54 | 14 | S | 73.56 | 1 | p<0.001 * |
| S+A+Pu | 58.63 | 14 | Pr | 89.74 | 1 | p<0.001 * |
| S+A+Pr | 38.52 | 14 | Pu | 49.52 | 1 | p<0.001 * |
| S+Pu+Pr | 47.19 | 14 | A | 66.86 | 1 | p<0.001 * |

SxPr dropped from model because it was too highly correlated with other variables.

S, CCL in 5 cm size increments commencing at 70 cm. A, Pu, Pr are dummy variables for adult, pubescent and prepubescent maturity status respectively; cross product variables were formed between each of the maturity classes and S. LR, log-likelihood ratio; * source makes a significant contribution to sex ratio.

on nesting beaches outside of Moreton Bay, no *C. caretta* tagged on the Moreton Banks or Maroon Banks has been reported from outside of the study site.

The size class distribution of the 320 turtles is summarised in Fig. 2. They ranged in size from immature (CCL = 70.1cm) to adult (CCL = 104.5cm) turtles. There were no turtles captured in the size range between that of hatchlings (approximate CCL = 4cm, Limpus, 1985; Limpus et al., 1984) and large immatures with CCL = 70cm. Most were large immature turtles (CCL = 70 - 90cm).

Sex and maturity was determined for 272 individuals. The population structure by sex, size and maturity is summarised (Fig. 2, Table 2). Only two of these turtles were not clearly male or female with respect to gonad development and were considered to be intersex animals. These intersex turtles are not considered in the sex ratio analysis.

Stepwise unweighted logistic regression showed that sex ratio was variable within the population, being significantly correlated to maturity status and size class of the turtles (Table 3): female proportion = $6.668M_1 + 6.913M_2 + 10.616M_3 - 0.19393 \cdot \text{size}$ (where $M_1 = 0$ for adults, $M_1 = 1$ for non adults; $M_2 = 0$ for pubescent immature turtles, $M_2 = 1$ for non pubescent immature turtles; $M_3 = 0$ for prepubescent turtles, $M_3 = 1$ for non prepubescent turtles; size denotes 5cm increments in curved carapace length beginning at 70cm; female proportion denotes the proportion of females in the subset.)

The combined *C. caretta* population inhabiting the Moreton and Maroon Banks comprised 35.2% females (95% confidence limits 5.7%, i.e. a sex ratio of 0.54:1, female to male). This pooled sex ratio is significantly different from 1:1 ($\chi^2 = 23.7$, $df = 1$, $p < 0.001$).

The mean size of these turtles by maturity status is summarised (Table 4). Of the 95 females examined for sex and maturity, there were 38% adult, 35% pubescent immature and 27% prepubescent immature turtles. The mean size (CCL) of adult females was 92.5cm, of pubescent females was

84.9cm and of prepubescent females was 78.4cm. Of the 175 males similarly examined, there were 27% adult, 8% pubescent immature and 65% prepubescent immature turtles. The mean size (CCL) of adult males was 96.1cm, of pubescent males was 90.6cm and of prepubescent males was 81.9cm.

There was no distinct carapace size class that separated adults from immature turtles for either sex (Fig. 2). For both sexes there were immature turtles larger than the mean size of the adults (Table 4). The adult males were significantly larger than the adult females ($t_{1,82} = 11.72$, $p < 0.001$).

Forty-eight turtles were weighed (Fig. 3). Because the log/log regression equations of CCL against weight by sex were coincident, the data was pooled for all turtles. This gave a significant correlation between size and weight of the turtles: $\log(WT) = 3.1655 \log(CCL) - 4.2416$ ($r^2 = 0.889$; $F = 368.4$ $df = 1, 46$).

While there were significant differences in tail length of adult males and females, there was considerable overlap in the tail lengths of immature male and female turtles and some adult female turtles (Fig. 4). In this sample, all turtles sexed by gonad examination that had TLC > 1.0cm were males and all turtles with CCL > 88cm and TLC < 1.0cm were female. Based on this sample, *C. caretta* with CCL 88cm and TLC 1.0cm could not be reliably sexed using external measurements.

The frequency distribution by breeding status of adult females is summarised by year in Table 5. No

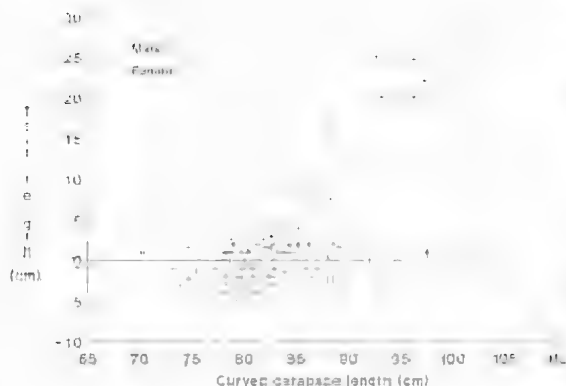


FIG. 4. Scatter plot of carapace length (CCL) against tail length from the carapace (TLC) for *Caretta caretta* captured on the Moreton and Maroon Banks of Moreton Bay.

adult female examined in the present study showed evidence of breeding in two consecutive breeding seasons. The results as presented in Table 5 have included young adults that have not yet recruited to the breeding population but whose reproductive system is structurally indistinguishable from that of adults that have bred successfully in the past, except for the absence of corpora albucantia. There was no significant difference in the proportion of adult female *C. caretta* that bred from this feeding area in the three breeding seasons 1989 - 1992 ($\chi^2 = 2.224$, $df = 2$, $p = 0.33$). The mean proportion of the adult females that bred in any one year was 0.20 (95% confidence limits = 0.09).

A total of 55 turtles showed evidence of anthropogenic injuries and/or health problems. Twenty turtles (6.3%) appeared to be in poor health as evidenced by their leanness and plastron concavity (mean CCL = 79.7cm, SD = 4.73, range = 70.3-88.1, $n = 19$). One turtle (0.3%) had curvature of the spine (scoliosis; prepubescent male, CCL = 88.9cm). Injuries resulting from anthropogenic causes were recorded for 6.9% of the turtles: 17 (5.3%) with healed or healing propeller cuts to the carapace (9 adult, 1 pubescent, 6 prepubescent turtles; mean CCL = 90.6cm, SD = 8.06, range = 75.6-102.3, $n = 17$) and 5 (1.6%) with healed or healing carapace fractures consistent with having been hit by a boat or having been dropped on the sorting tray of a trawler (all prepubescent turtles, mean CCL = 81.5cm, SD = 2.01, range = 79.3-85.0, $n = 5$). The closeness and length of cuts on the turtles recorded with propeller damage were consistent with damage that could be inflicted by small

outboard motors. Fibropapillomas were present on 14 turtles (4.4%; 8 adult, 4 pubescent, 2 prepubescent; mean CCL = 90.9cm, SD = 5.60, range = 80.3-99.2, $n = 14$). If fibropapillomas are a consequence of pollution (Balazs & Pooley, 1991), then 10.7% of the turtles displayed evidence of anthropogenic impacts.

The majority of these turtles carried substantial numbers of epifauna and epiflora on their carapaces and to a lesser extent on the flippers, head and plastron. The Turtle Barnacle (*Chelonibia testudinaria*) and an oyster (*Ostrea* sp.) were the most obvious common commensal faunal species on the carapace of these turtles. The mean number of large *C. testudinaria* (barnacles larger than 1cm in diameter) per carapace was 6.8 (SD = 14.0, range = 0 - 94, $n = 296$). The other barnacles included *Stomatolepas praegustator* (in the buccal cavity and skin folds at the base of the neck and groin), *Platylepas decorata* (mostly on the skin of neck and flippers), *Tubicinella cheloniae* (burrowed into the dorsal carapace and ventral surface of the posterior marginals) and *Balanus trigonus* (on the carapace). Other species of oyster regularly found attached to the dorsal surface of the carapace included *Pinctada margaritifera* and *Saccostrea cucullata*. Other commensal fauna included worms (polychaetes and parasitic leeches, *Ozobranchus margo*), *Cunjevoi* (*Pyura stolonifera*) and other smaller ascidians, amphipods and crabs. The gastropod *Thalotia marginata* was occasionally found grazing on the algal turf growing on the carapace. Conspicuous algae growing on the carapace included *Enteromorpha intestinalis*, *Ulva* sp. and *Gracilaria edulis*. Schools of small Golden Trevally (*Gnathanodon speciosus*) often were seen swimming immediately in front of the snout of swimming turtles and feeding around foraging turtles.

Six turtles were captured which lacked the epifauna and epiflora that characterise the *C. caretta* resident in this study site. These turtles appeared to be 'clean' and more striking in their colouration; all had intensely black tomia within the buccal cavities; all were small turtles (mean CCL = 79.8cm, SD = 2.71, range = 74.9-83.0, $n = 6$); all were prepubescent immature; 4 males, 2 unsexed. These turtles are interpreted as having recently recruited to residency in the feeding area and had not as yet acquired the local epizoon and epiphytic organisms. One of these new recruits was the only turtle recorded during the study that had open but healing wounds from a recent mauling from a shark.

TABLE 4. Size of *Caretta caretta* from eastern Moreton Bay by sex and maturity status.

| | Maturity | Curved carapace length (cm) | | | |
|--------|--------------|-----------------------------|-------|------------|-----|
| | | mean | s.d | range | n |
| Female | adult | 92.51 | 5.263 | 82.2-103.5 | 36 |
| | pubescent | 84.89 | 4.542 | 79.0-102.8 | 33 |
| | prepubescent | 78.43 | 3.728 | 70.1-85.7 | 26 |
| Male | adult | 96.12 | 4.388 | 85.1-104.5 | 48 |
| | pubescent | 90.55 | 4.058 | 84.8-96.5 | 14 |
| | prepubescent | 81.87 | 4.202 | 70.3-95.2 | 113 |

Many of the turtles were observed digging shallow broad depressions in the substrate with a sweeping action by the front flippers, thus creating a low vertical wall in front of the turtle. Given that the stomach contents of stranded turtles in adjacent areas include large quantities of a number of species of bivalve molluscs that burrow into the substrate (Razor Clam, *Pinna bicolor*; Mud Ark, *Anadara trapezia*; Chinese Fingernail Shell, *Solen grandis*; unpubl. data), it is presumed that the *C. caretta* observed digging these depressions were actively foraging. Recently worked feeding depressions are a common sight over the Moreton Banks. Similar feeding behaviour was observed with *C. caretta* at this study site in 1989 (T. Preen, pers. comm.). Not all feeding involved digging for prey items: an adult male, CCL = 94.2cm, was seen feeding on the anemone *Stichodactyla haddoni* while a large immature turtle was captured with a Blue Swimmer Sand Crab (*Portunus pelagicus*) in its mouth. As was observed with *C. mydas* feeding over the same banks, the foraging *C. caretta* tended to move in across the intertidal flats with the rising tide and fall back to deep water with the ebbing tide.

DISCUSSION

Old confirmed records of *C. caretta* from Moreton Bay have been difficult to locate. The oldest specimen record is a Queensland Museum specimen from the Bay that was registered in 18 August 1964 (QMJ13183: from Sandgate, dentary only, originally registered as *Eretmochelys imbricata*). Backhouse (1843) talks of three species of turtles in Moreton Bay but does not identify which ones. There had been a *C. mydas* fishery in Moreton Bay spanning at least 50 years from the 1890s (Limpus et al., 1994). However, until the 1960s there appears to be no published recognition of *C. caretta* in Moreton Bay. This reflects that the species was perceived as insignificant

compared to *C. mydas* which had economic and nutritional values. In contrast with *C. mydas* populations in Queensland (Limpus et al., 1994), there is no indication that *C. caretta* in Moreton Bay or elsewhere in Queensland were subjected to intense harvest in the past.

The Moreton Bay area is the southern limit for annual successful nesting for the species. Further south, nesting is not an annual event although nesting by *C. caretta* has been confirmed from as far south as Ballina, NSW (unconfirmed records from as far south as Newcastle, 33°S) while the large nesting populations occur to the north of Moreton Bay (Limpus, 1985). Bowen et al. (1994) have identified this eastern Australian breeding assemblage as the only significant *C. caretta* breeding population for the South Pacific Ocean. Further, they demonstrate that the eastern Australian population is genetically distinct from the population breeding in the North Pacific. While small numbers of *C. caretta* (probably 1-3 individuals) nest each year on the seaward beaches of North Stradbroke and Moreton Islands (Limpus, 1985; Limpus & Couper, unpubl. data), none of these nesting turtles have been tagged. It is thus not possible at present to determine if any of the local nesting is by adult females that live year round in Moreton Bay or whether they are turtles undertaking breeding migrations from more distant feeding areas. Given the low level of local nesting, we conclude that the majority of



FIG. 5. Annual fluctuations in the breeding rate, measured as the proportion of adult females that prepared for breeding for the year, of *Caretta caretta* resident in two feeding grounds in eastern Australia (Heron-Wistari Reefs: Limpus & Reimer, 1994. Moreton Bay: present study). These fluctuations are compared with the fluctuations in the number of *Caretta caretta* that have bred annually at the Mon Repos and adjacent rookeries of the Woongarra coast (Limpus & Reimer, 1994).

TABLE 5. Frequency distribution by breeding status and breeding season for adult female *Caretta caretta* recorded from Moreton Bay during the study period. Adult females were identified by gonad examination following Limpus (1985, 1992b) or by having been recorded laying eggs at a distant rookery during the current breeding season.

| Breeding season | Adult | | | | Total |
|-----------------|-----------------------|---------------------------|---------------------------|-------------------------------|-------|
| | Breeding ¹ | Non-breeding ² | Pre-breeding | | |
| | | | Vitellogenic ³ | Non-vitellogenic ⁴ | |
| 1989/90 | 5 | 17 | 0 | 1 | 23 |
| 1990/91 | 4 | 21 | 1 | 5 | 31 |
| 1991/92 | 7 | 10 | 2 | 5 | 24 |

¹ adults that bred (ovulated) in the current breeding season.

² adults that have ovulated in previous breeding seasons as indicated by the presence of corpora albucantia 3 mm and which did not breed in the current breeding season.

³ adults that have yet to breed (no corpora albucantia) and the vitellogenesis for the current season did not result in ovulation.

⁴ adults that have yet to breed (no corpora albucantia) and were non-vitellogenic for the season.

C. caretta that live in Moreton Bay migrate elsewhere to breed. Based on tag recoveries (Table 1), the present study indicates that most of the resident turtles can be expected to migrate to breed on mainland beaches of the Bundaberg coast, with only a small proportion of the Moreton Bay residents migrating to nest on the islands of the southern GBR. Moreton Bay is a significant feeding ground for the eastern Australian nesting *C. caretta*.

The high incidence of recaptures of individual turtles within a localised feeding area and the absence of recaptures elsewhere, except for breeding migrations (present study; Limpus, 1985, 1989, 1991; Limpus & Reimer, 1992; Limpus et al. 1992), indicate that there is little or no substantial movement of *C. caretta* between widely separated feeding areas. The limited number of recaptures available (tag numbers X28101, T22706, T41196) show that Moreton Bay resident females have a high fidelity to this feeding area to which they return following a breeding migration (Limpus, 1989; Limpus et al., 1992; present study).

As for the resident feeding population on the coral reefs of the southern GBR, the *C. caretta* population living on the Moreton Banks is comprised only of large immature and adult turtles (Limpus, 1985). The smallest turtle captured in the present study was 70.1cm and the smallest beachwashed specimen reported from the Moreton Bay area during the period of the present study had a CCL = 62.5cm (QM J55131). Post hatchling *C. caretta* (i.e. CCL = 4-30cm) are

rarely encountered in eastern and northern Australia except on the ocean beaches adjacent to Moreton Bay and in northern NSW when strong onshore winds strand small *C. caretta* post hatchlings (CCL = 4-10cm) during March - May (Limpus, Walker & West, 1994; Limpus & Couper, unpubl. data). It is presumed that these young *C. caretta* were travelling south in the East Australian current from the major rookeries of south Queensland (Walker, 1994). The authors know of only a few isolated records of small immature *C. caretta* (CCL = 30-70cm) in Australian waters (Limpus, Walker and West, 1994). The present study indicates that immature *C. caretta* recruit to reside in the Moreton Banks feeding

ground at a mean CCL = 79.8cm. The total absence of coastal epifauna and epiflora on the turtles identified as new recruits suggests that this size range of *C. caretta* is recruiting from open ocean habitat(s).

Once young turtles recruit to the Moreton Banks, they remain as residents and all size classes occur from the small immatures (CCL = ~70 cm) up to large adults of both sexes. These *C. caretta* occur on the Moreton Banks all year round and within the shallow subtidal and intertidal feeding areas these *C. caretta* are primarily carnivorous. The resident population is strongly biased to males (64.8%) and to immature size classes (62% of females, 73% of males). The resident *C. caretta* of the coral reefs of the southern GBR are also significantly biased to males (Limpus, 1985). This contrasts with the strong bias to females (66%) recorded for the *C. mydas* resident on the Moreton Banks (Limpus et al., 1994). Sexual maturity for both sexes does not usually occur at the minimum breeding size but at some larger size. The adult females recorded from the Moreton Banks were not significantly different in size from those resident on the coral reefs adjacent to Heron Island in the southern GBR (Limpus, 1985. One way ANOV: $F = 2.2$; $df = 1,55$; $0.5 > p > 0.2$). the only other site in eastern Australia where foraging adult *C. caretta* have been measured. In contrast the adult females foraging on the Moreton Banks are significantly smaller than the nesting females on the Bundaberg coast (Limpus, 1985. One way ANOV: F

= 19.0; df = 1,2241; $p > 0.5$). This suggests that there are other feeding grounds that supply the larger sized nesting females to the Bundaberg coast. The adult males resident on the Moreton Banks were not significantly different in CCL when compared to the small sample of adult males captured at courtship in the southern GBR (Limpus, 1985. One way ANOV: $F = 0.095$; $df = 1,53$; $p > 0.5$).

The proportion of adult females that prepared for breeding from the Moreton Bay feeding area was consistently higher in each year, 1989-1991, than the proportion that prepared to breed from the Heron-Wistari Reefs feeding area of the southern GBR in the same years (Fig. 5). The proportion of females that prepared to breed each year from the Moreton Bay feeding area did not parallel the decline in nesting females recorded at Mon Repos and adjacent rookeries on the Woon-garra coast (Fig. 5) and at other eastern Australian rookeries (Limpus & Reimer, 1994). This adds further weight to the argument that the eastern Australian decline in *C. caretta* nesting numbers is not the result of annual fluctuations in the proportion of turtles migrating from the feeding areas but is an index of the overall reduction in the total population within the southwestern Pacific Ocean foraging range for the species (Limpus & Reimer, 1994).

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PSEUDOCEROS AND PSEUDOBICEROS (PLATYHELMINTHES, POLYCLADIDA, PSEUDOCEROTIDAE) FROM EASTERN AUSTRALIA AND PAPUA NEW GUINEA

LESLIE J. NEWMAN AND LESTER R.G. CANNON

Newman L.J. & Cannon L.R.G. 1994 12 01: *Pseudoceros* and *Pseudobiceros* (Platyhelminthes, Polycladida) from eastern Australia and Papua New Guinea. *Memoirs of the Queensland Museum* 37(1): 205-266. ISSN 0079 - 8835.

The large tropical polyclad genus *Pseudoceros* Lang, 1884 is reviewed and of the over 150 species recognised by Faubel (1984) and Prudhoe (1985, 1989) only 26 are considered members of *Pseudoceros* sensu stricto. *Pseudobiceros* Faubel, 1984 is upheld and 14 species are recognised. For the Great Barrier Reef and eastern Papua New Guinea, 23 *Pseudoceros* (17 new species) and 11 *Pseudobiceros* (8 new species) have been found. Collectively these polyclads are not uncommon on coral reefs and feed mainly on colonial ascidians. Observations on feeding and copulatory behaviour, and larval development are given. The simple hypodermic insemination observed in these animals supports anatomical analyses that clearly demonstrates intraspecific homogeneity of the reproductive structures within species of a genus. Genera may be determined on gross morphology of the pseudotentacles, eyes, pharynx and number of male pores. Specific determinations rely primarily on colour pattern, as suggested by Hyman (1954, 1959a) and Prudhoe (1985). □ *Polycladida*, *Cotylea*, *Pseudocerotidae*, *Pseudoceros*, *Pseudobiceros*, flatworm, taxonomy.

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Large, flamboyantly coloured flatworms have been known from tropical seas, and especially from coral reefs for nearly 150 years (Prudhoe, 1985); most have been assigned to *Pseudoceros* Lang, 1884 (Polycladida). These species have been recorded from few specimens, often only a single one, and sometimes only from coloured paintings (Schmarda, 1859; Lang, 1884; von Graff, 1893; Stummer-Traunfels, 1933). More often than not, type specimens have not been designated and specimens have rarely been deposited in museums. A serious contributing factor to their poor representation in collections is the ability of these worms to self-destruct under stress. Before fixation is complete, worms often autolyse, breaking into mucous fragments, or contract and contort making examination impossible; and most invariably have lost their colour and pattern.

Despite this, Marcus (1950) and Hyman (1954, 1959a) listed over 100 species of *Pseudoceros* distinguished primarily on colour and pattern. Although details of the reproductive anatomy are the most widely used characters for classifying turbellarian flatworms (Cannon, 1986) only about 25 worms assigned to *Pseudoceros* have been investigated in this way. Both Hyman (1954, 1959a) and Prudhoe (1985, 1989) maintained that within *Pseudoceros* only colour pattern is required to distinguish species, so lack of

reproductive details has not been considered an impediment to the erection of new species.

A contrary view was proposed by Faubel (1984) who based his classification of the polyclads largely on anatomical characters, mainly of the male reproductive system. Faubel erected several new genera to accommodate *Pseudoceros* sensu lato and these are distinguished on details of the male reproductive system. Prudhoe (1985, 1989) disagreed believing, for example, that the number of male complexes (one or two) could vary within species. He was influenced largely by the view of Lang (1884) that *P. maximus* was found in the Bay of Naples with three variations: either one or two separate male complexes or two male complexes opening into one antrum.

No comprehensive taxonomic account of free-living marine flatworms from Australian waters exists. Polyclads have not received attention although they are conspicuous reef inhabitants (Hyman, 1954; 1959a; Prudhoe, 1985; 1989; Newman & Cannon, 1994); are symbionts and pests of a variety of reef invertebrates (Prudhoe, 1985), including giant clams (Newman et al., 1993) and soft corals (Cannon, 1990); and are mimics of toxic nudibranchs (Newman et al., 1994). Less than 20 studies have considered Australian polyclads, several are popular or deal with them as pests (Stead, 1907) or potential parasite vectors (Anderson et al., 1993) and only

seven taxonomic papers have been published since 1898 (Woodworth, 1898; Haswell, 1907; Hyman, 1959b; Prudhoe, 1977; 1982; Cannon, 1990; Newman et al., 1994). Of the 16 nominal species recorded from the GBR only three have been described as new in that time (Cannon & Newman, 1993).

This study set out to examine the tropical '*Pseudoceros*' fauna from the Great Barrier Reef (GBR) and eastern Papua New Guinea (PNG). We wanted to ascertain the relative merits of the proposals of Faubel (1984) and Prudhoe (1985) for the determination of genera and species within *Pseudoceros* sensu lato by making use of observations of live animals, in situ photography and examination of new taxonomic characters. We were significantly assisted by the development of a new fixative regime (Newman & Cannon, in press) which produces consistently well fixed, flat specimens with minimum loss of colour pattern.

METHODS

Animals were either hand collected from under coral boulders at the reef crest or under ledges on the reef slope by SCUBA from Heron Island (23° 27' S, 151°55' E) and One Tree Island (23°30' S, 152°05' E) southern GBR and Madang (5°14' S, 145°45' E) and Laing Island (4°16' S, 144°56' E), eastern Papua New Guinea. Unless otherwise stated all animals were collected during the day and photographed by L.J. Newman and A.E. Flowers. Flatworms were kept in separate containers and brought back to the laboratory live, and retained in 1 litre plastic ice cream containers (non-aerated to avoid physical damaged to these delicate worms from the bubbles). Photographs were taken either in situ using Nikonos III & V cameras, extension tubes and underwater strobes, or in the laboratory using Nikon F4 and Canon T70 & T90 with 50 & 105mm macro lenses, extension tubes and TTL flashes.

Full details of specimen fixation and preparation are given by Newman & Cannon (in press). In brief, polyclads were fixed by coaxing them onto filter paper which was then transferred to frozen fixative (formaldehyde, calcium acetate - propylene glycol, propylene phenoxylol). After fixation for 12 to 24 hours, specimens were preserved in 70% ethanol for histological preparation. Whole mounts were prepared by first staining with Mayer's Haemalum, then dehydrating in graded alcohols and mounting in canada balsam. Longitudinal serial sections of the

reproductive region were prepared by embedding excised tissue in Paraplast (56°C), sectioning at 5 - 7µm, and staining with haematoxylin and eosin. Only mature animals were prepared for serial sections and wholemounts, when possible.

Drawings and measurements were made with the aid of a camera lucida by L.J. Newman. Measurements given in descriptions are from type specimens. These provide a guide to relative size of animals but because of the plasticity of form, differences in specimen size cannot be considered absolute. Body measurements are expressed in mm (length x width) and were taken from live animals in a relaxed state. Abundance data are expressed as the number of animals collected: R = rare, 1 - 5 animals; C = common, 6 - 20 animals; A = abundant, > 21 animals. Presentations of the reproductive anatomy derived from sections are given with minimal interpretation and, as far as practical, are taken directly from single sections. Only one side of the reproductive apparatus was drawn for *Pseudobiceros*.

Descriptions of colour patterns are based on living animals. Colours and colour number in parenthesis refer to Pantone Colors by Letraset 1989 Series U. Unless otherwise stated all material and colour transparencies are lodged at the Queensland Museum (QM): wet specimens in 70% ethanol are designated (S), wholemounts (WM), serial sections (LS) and colour transparencies (CT). Material examined from other institutions includes that from the British Museum (BMNH), United States National Museum (USNM) and the Australian Museum (AM).

Legends for all figures are as follows: a, auricular groove; c, cement glands; ce, cerebral eyespot; cp, cement pouch; e, ejaculatory duct; f, female pore; i, intestine; m, marginal ruffling; ma, male pore; mo, mouth; o, oviducts; p, pharynx; pe, pseudotentacular eyes; pr, prostate; ps, pseudotentacles; s, sucker; sc, scattered ovaries & testes; se, seminal vesicle; st, stylet; v, vas deferens; va, vagina.

TAXONOMY

THE PROBLEM WITH *PSEUDOCEROS*

Pseudoceros is the dominant genus within the family Pseudocerotidae which contains about 200 species in seven genera. Pseudocerotids are characterised and distinguished by a ruffled pharynx from the next most speciose family of tropical polyclads, the Euryleptidae, which have

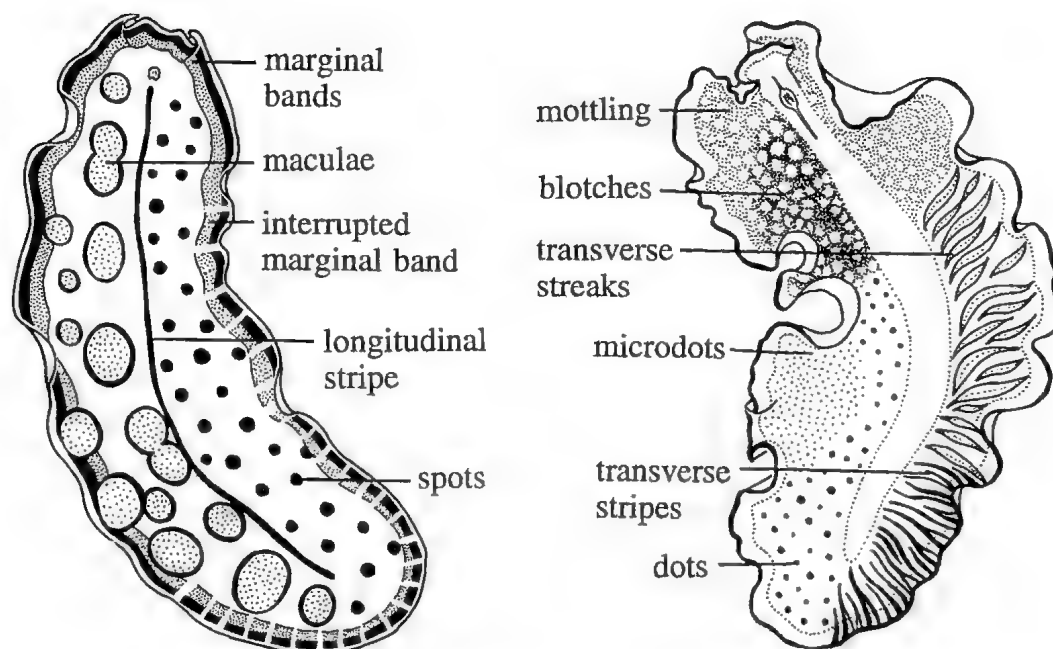


FIG. 1. Dorsal surface colour patterns found in *Pseudoceros* and *Pseudobiceros*.

a tubular pharynx (this latter family has about 130 species in 12 genera; Prudhoe, 1985). The other genera of pseudocerotids are less speciose (most are monospecific) and poorly known (Cannon, 1986).

Genera within the Pseudocerotidae are distinguished by characteristics of the male reproductive system (presence or absence of prostate and seminal vesicle), the female system (number of complexes), the alimentary system (presence or absence of anal pores) and external characters (presence or absence of dorsal papillae and tentacular eyes).

According to Prudhoe (1985, 1989) *Pseudoceros* is by far the biggest genus with about 150 named species (75% of the family). Marcus (1950) listed all known species distinguished on colour pattern alone. Both Hyman (1954, 1959a) and Prudhoe (1985, 1989) considered reproductive anatomy too homogeneous within the genus to be useful in classification and reaffirmed the belief that within *Pseudoceros* species determination could be made solely on the basis of colour pattern. Prudhoe (1985) further pointed out that although colours fade on preservation or change through diet (Crozier, 1917), the pattern still remained.

It is well established among turbellarian flatworms (and probably within the phylum

Platyhelminthes) that the anatomy of the reproductive system is of major significance in classification (Cannon, 1986). Basing his work substantially on reproductive anatomy, Faubel (1984) erected a new scheme for the Polycladida at variance with the more conventional view of Lang (1884), Bresslau (1933) and Marcus and Marcus (1968) which Prudhoe (1985) continued to follow. A consequence of this was the separation of *Pseudoceros* into five genera. Working mainly from the literature Faubel (1984) found it difficult to assign many taxa to these new genera and so established a list of incertae sedis. Prudhoe (1985, 1989) knew of Faubel's work and rejected it, maintaining variability was an inherent part of *Pseudoceros* and that changes due to maturation could also be reflected in differential morphology of some organs.

We analyse here some of the characters (established and new) within *Pseudoceros* sensu lato which we believe can elucidate the taxonomy of this large genus. Although the genus was split by Faubel (1984), the genera other than *Pseudoceros* were not accepted by Prudhoe (1985, 1989). However, we have ascertained that by examining extensive material from the GBR and PNG, the genus *Pseudobiceros* Faubel, 1984 is valid. Based on our re-examination of these two genera we find we can only reliably place a limited

TABLE 1. Colour pattern groups for recognised and new species of *Pseudoceros*.

| | Colour Pattern | Recognised Species | New Species |
|---|------------------------------|--|--|
| 1 | Even Colour | <i>perviolaceus</i> - purple | <i>bolool</i> - black |
| 2 | Marginal Bands | <i>bimarginatus</i> * - white; orange & black & yellow margin <i>gamblei</i> - white; blue margin <i>litoralis</i> - brown; orange & black margin | <i>depiliktatub</i> - black; green & cream & yellow margin <i>jebborum</i> - orange; black & orange margin <i>periauranti</i> - black; orange margin <i>peripurpureus</i> - black; violet & purple margin <i>prudhoei</i> - brown; blue & yellow margin <i>sapphirinus</i> - black; blue lateral band <i>verecundus</i> - cream; orange & black interrupted margin |
| 3 | Longitudinal Stripes | <i>bifasciatus</i> - purple; 2 black stripes, orange & white margin <i>bifurcus</i> - blue; 1 median stripe, orange & white margin <i>dimidiatus</i> * - black; 2 yellow stripes, orange margin <i>gravieri</i> * - blue; many yellow stripes <i>violaceus</i> - purple; 1 yellow median stripe, yellow margin <i>kelaartii</i> - purple mottled; 3 white stripes <i>tristriatus</i> - blue, 3 orange stripes | <i>laticlavus</i> - black; 1 median white stripe, white margin <i>monostichos</i> - cream; narrow black median line, blue & purple & green margin <i>paralaticlavus</i> - black; 1 median white stripe, white & yellow margin |
| 4 | Spots, Dots & Mottling | <i>atropurpeus</i> - purple; white dots <i>concinus</i> - cream; blue spots <i>ferrugineus</i> - red; white dots <i>interruptus</i> - brown mottled, blotches of red-brown, interrupted margin <i>leptostictus</i> * - cream; orange & black spots, interrupted margin <i>memoralis</i> - white; brown dots & interrupted margin <i>mossambicus</i> - black; greenish spots <i>pardalis</i> - brown; yellow spots <i>pius</i> - yellow mottled; red & black spots <i>vinosus</i> - red; yellow & white dots | <i>goslineri</i> - cream & brown mottling; pink & purple spots & dots <i>heronensis</i> - cream; brown & white dots, yellow margin <i>ouini</i> - cream mottled; pink spots at margin |
| 5 | Maculae | <i>glaucus</i> - grey; black maculae | <i>lindae</i> - burgundy; yellow & blue maculae <i>scintillatus</i> - black; yellow maculae, orange margin |
| 6 | Transverse Streaks & Stripes | <i>zebra</i> - yellow; black streaks, orange margin | <i>felis</i> - grey mottled; black bifurcating stripes & spots |
| † | Colour indeterminate | <i>fuscogriseus</i> , <i>langemaakensis</i> , <i>tomiokensis</i> | |

*collected during this study, † colour pattern not given in original description, but sufficient detail provided from preserved specimens for generic determination.

number of species in each. A discussion of morphological and anatomical characters is given here for *Pseudoceros* and comparisons are made with *Pseudobiceros*.

Colour & pattern. Due to incomplete species descriptions in the past literature, we have defined and illustrated colour patterns for both *Pseudoceros* and *Pseudobiceros* based on living animals (Fig. 1). We have created six groups of colour patterns to aid in species identifications and comparisons are made where possible with the previous literature (Tables 1, 2). Although these divisions may be somewhat arbitrary, they provide a basis for the description of these flatworms.

Pseudoceros contains the most diversified colour groups and the colour patterns are usually

opaque. The majority of species were found to be spotted, dotted or mottled (Group 4). Species with an even background colour (Group 1) and distinct maculae (Group 5) were not common. In contrast, the majority of *Pseudobiceros* were flamboyantly patterned either possessing a dark (usually black) background with distinct marginal bands (Group 2) or stripes (Groups 3 & 6). It appears that *Pseudobiceros* are generally more strikingly coloured when compared to *Pseudoceros* which possesses many cryptically coloured species.

The ovaries are sometimes bright red or deep purple and can influence the colour of the dorsal surface. The pharynx, intestine and reproductive organs are white in both genera.

Shape, texture & size. Both genera are extremely delicate, elongate oval and have a smooth

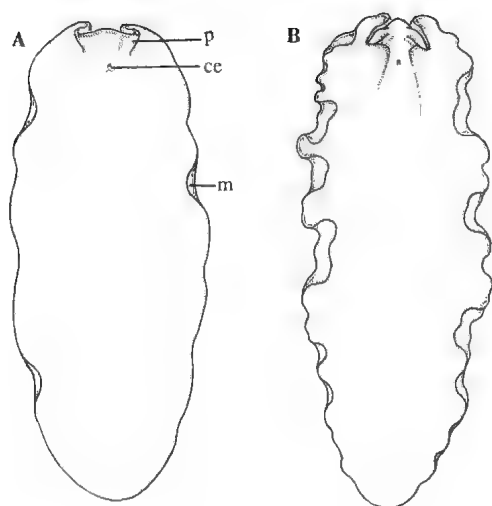


FIG. 2. General morphology of the dorsal surface. A, *Pseudoceros*; B, *Pseudobiceros*.

dorsal surface without dorsal papillae as found in *Acanthozoon* and *Thysanozoon*.

Pseudoceros are flat with few, shallow marginal ruffles (tending to increase in number with size) and blunt posteriorly or tapering only slightly when extended (Fig. 2A). Species range in size from a few millimetres (juveniles) to a maximum of 70×35 mm. In contrast, *Pseudobiceros* are narrower, raised medially, possess deep marginal ruffles (often crenulated when the animal is resting) and taper posteriorly when extended (Fig. 2B). Most species are extremely fragile and readily fall apart when disturbed. Species which are black or mainly black are opaque but most other species are transparent and their internal organs can be seen through the epidermis. *Pseudobiceros* are undoubtedly the largest of the pseudocerotids reaching a maximum of 140×80 mm; twice the maximum size of *Pseudoceros*.

Pseudotentacles. The 'tentacles' are clearly folds of the anterior margin and not separate as in Euryleptidae. These pseudotentacles must be examined from living animals as they lose their distinctive shape during fixation.

In *Pseudoceros*, the pseudotentacles are simple folds occurring in two forms; either square blunt, simple, tubular folds (Fig. 3A) or pointed broad flaps (Fig. 3B). It appears that differences between these two forms are due to size since both forms have been observed in a single species. Conversely in *Pseudobiceros*, the pseudotentacles are further developed, held more erect and are more conspicuous. Two distinct pseudoten-

tacular types are found being either ear-like and pointed (Fig. 3C) or square with lateral ruffles (Fig. 3D). The degree of lateral ruffling of the pseudotentacles can also vary from slight to deep ruffles. Differences observed between these two forms of pseudotentacles in *Pseudobiceros* are species specific.

Cerebral eyes. Prudhoe (1989) noted that the number of eyes increased with size. Within the cerebral eyespot the eyes are arranged in a horse-shoe shaped cluster with concentric rows (not two distinct elongate clusters as found in Euryleptidae). There is little difference in the arrangement of cerebral eyes between *Pseudoceros* and *Pseudobiceros* although the latter tends to possess a larger number of eyes, especially in mature animals. Occasionally the cerebral eyes appear to form a round cluster in both genera.

The cerebral eyespot is often found in the clear area which in *Pseudoceros* is an inverted heart shape (Fig. 3A, B) and in *Pseudobiceros* an elongate oval extending anterior and posteriorly, sometimes becoming an indistinct median line in large specimens (Fig. 3C, D). The presence and shape of this clear area is evident in live animals but lost during fixation. Occasionally a few precerebral eyes are found in *Pseudoceros*.

Pseudotentacular eyes. Pseudotentacular eyes are present in both genera (not absent as in *Parapseudoceros*) although they are difficult to see in animals with black backgrounds or marginal bands. The dorsal pseudotentacular eye arrangement differs between *Pseudoceros* and *Pseudo-*

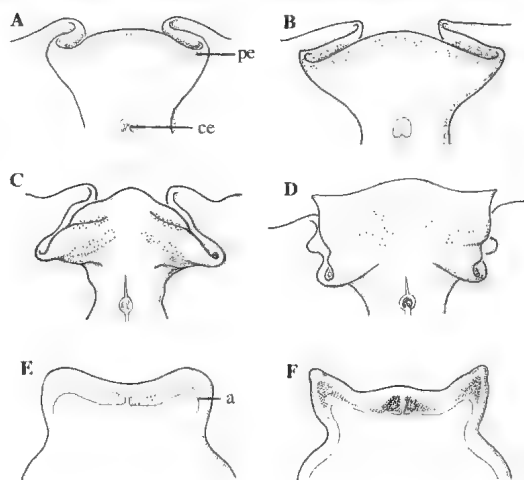


FIG. 3. A-D, Dorsal pseudotentacles and eye arrangement. A, B, *Pseudoceros*; C, D, *Pseudobiceros*. E, F, ventral pseudotentacular eye arrangement. E, *Pseudoceros*; F, *Pseudobiceros*.

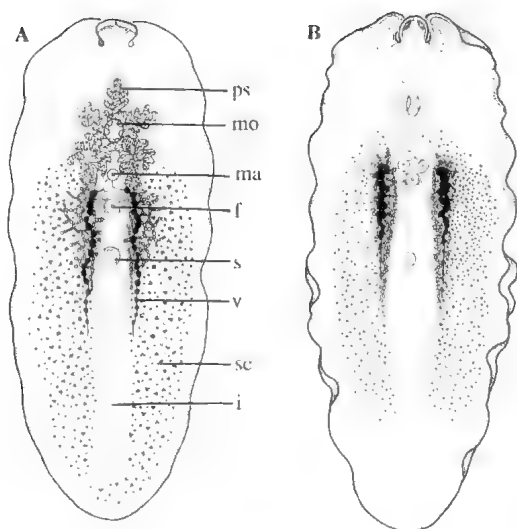


FIG. 4. General morphology of the ventral surface. A, *Pseudoceros*; B, *Pseudobiceros*.

biceros: in *Pseudoceros*, the dorsal pseudotentacular eyes are arranged in two to three scattered lines across the anterior pseudotentacular rim (Fig. 3A, B), but in *Pseudobiceros* the eyes are arranged in four loose longitudinal clusters across the pseudotentacles (Fig. 3C, D). The ventral pseudotentacular eyes occur in two loose clusters in *Pseudoceros*, but in four dense clusters in *Pseudobiceros* (Fig. 3E, F).

An auricular ciliated groove is found ventrally and terminates at the lateral limit of the pseudotentacles in *Pseudoceros* but extends laterally along the margin in *Pseudobiceros* (Fig. 3E, F). According to Prudhoe (1985) the function of this groove is unknown but it is probably used for chemoreception.

Pharynx. The pharynx is clearly ruffled in *Pseudoceros* and *Pseudobiceros* (not tubular as found in Euryleptidae and Prosthiostomidae). Hyman (1959a) first noted differences in pharynx shape in *Pseudoceros* and used the phrase 'butterfly shape' to describe a pharynx with 'lateral lobulations that increase in length in the antero-posterior direction'. Hyman further stated that pharynx shape may be decisive in species determination but this has not been investigated in any detail. Prudhoe (1989) apparently did not agree with Hyman and stated that differences in pharynx shape were simply due to growth whereby 'in a young worm the pharynx has a compact outline, but as the worm grows so the

pharynx finally assumes a butterfly shape'. Furthermore, Prudhoe believed that differences in pharynx shape within the genus could be due to fixation.

Our studies clearly show a difference in pharynx shape between *Pseudoceros* and *Pseudobiceros*. The pharynx in *Pseudoceros* is round and oval with about seven (one anterior, four lateral and two posterior) complex pharyngeal lobes, each dividing ('butterfly shaped') and extending laterally (Fig 4A, 5A). In comparison, the pharynx in *Pseudobiceros* is generally relatively smaller, narrower and elongate-oval with about 10 to 20 shallow simple pharyngeal folds which do not divide (Figs 4B, 5B). Obvious differences in pharynx shape between these two genera have probably been overlooked since the pharynx shape can be drastically distorted in preserved specimens.

Intestine. The intestine extends posteriorly to just near the posterior margin of the body in *Pseudoceros* (Fig. 4A): it does not extend as far in *Pseudobiceros* (Fig. 4B). Numerous lateral anastomosing intestinal branches can be seen clearly in *Pseudoceros* as they evenly branch off the intestine trunk. It is difficult to see the numerous lateral branches of the intestine in *Pseudobiceros* since the intestine is much wider and often inflated. These intestinal branches appear to be finer and more numerous than in *Pseudoceros* and do not extend to the posterior limit of the intestine. It should be noted that the majority of *Pseudobiceros* collected during this study were velvety black and anatomical details were difficult to see in whole mounts.

Sucker. The sucker (or adhesive organ) is characteristic of the cotyleans but is sometimes difficult to see in preserved specimens. Prudhoe (1985) maintained that the purpose of the sucker was not known. Our in situ observations clearly show that the sucker is used to adhere animals to their substrate and is not used during copulation.

In *Pseudoceros* the small, round sucker is found posterior to the female pore in the mid-body (or just anterior to the mid-line when animals are alive) (Fig. 4A). The sucker and gonopores are generally equally spaced. In *Pseudobiceros* the sucker is less pronounced and is well separated from the male and female gonopores (Fig. 4B). Specimens of both genera were occasionally found with two unequal sized suckers.

Gonopores. In *Pseudoceros* the single male pore is found between or just posterior to the last pair of pharyngeal folds and the female pore is clearly separated from the male pore (Figs 4A,

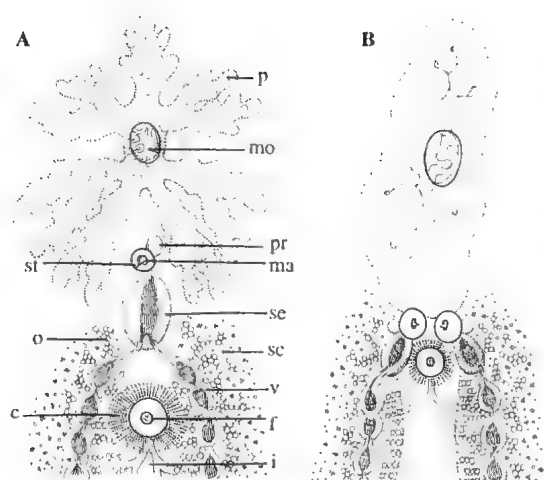


FIG. 5. Details of the pharynx and gonopores. A, *Pseudoceros*; B, *Pseudobiceros*.

5A). In *Pseudobiceros* the symmetrical male pores are found just posterior to the end of the pharynx (Figs 4B, 5B), and they are clearly separate. The two male antra and penis papillae are usually directed towards each other making interpretations of the penial stylet from longitudinal sections often difficult and several animals may need to be sectioned.

In *Pseudoceros* and *Pseudobiceros* there is a single female pore (not multiple as in *Nymphozoon*) found posterior to the male pore(s). In *Pseudoceros* the female pore is well separated from the male pore (Figs 4A, 5A) whereas in *Pseudobiceros* the female pore is clearly found between the male pores (Figs 4B, 5B). It should be noted that the position of the gonopores and sucker can change dramatically with fixation.

Testes. The scattered testes are found ventrally, occasionally occurring with the ovaries in the dorsal parenchyma (Prudhoe, 1985). Testes and ovaries often mature simultaneously.

Male pore(s). The presence of a double male reproductive system was first noted by Lang (1884). He described three varieties of *Pseudoceros maximus* Lang, 1884; one with a single male pore, one with two male pores and a double male apparatus, and one with two male systems but only one male pore. Stummer-Traunfels (1895) considered these three varieties to be different species but did not separate them. Later, Stummer-Traunfels (1933) figured two specimens of *Pseudoceros latissimus* (Schmarda, 1859), with one and two male pores.

Hyman (1959a) also noted that the presence of a single or paired male apparatus in *Pseudo-*

cerotidae was a useful character and predicted that the details of the male copulatory apparatus may be of value in specific diagnosis, but she rarely gave these details. Prudhoe (1989) maintained that the number of male copulatory apparatuses was questionable as a diagnostic feature. He explained that the occurrence of supernumerary of organs is well known among certain families of polyclads and he refrained from accepting Faubel's (1984) reclassification of the family Pseudocerotidae, including the diagnosis of *Pseudobiceros*, and instead recognised the systematics given by Bresslau (1933).

The double anatomy of the male reproductive system is characteristic of *Pseudobiceros* (Figs 4B, 5B). There can be no question that this represents merely supernumerary of male organs as suggested by Prudhoe (1989). Significant differences in other morphological characters (such as the pseudotentacles, eyes and pharynx) exists between *Pseudoceros* and *Pseudobiceros* to confirm the distinction between these genera.

Vas deferens. Prudhoe (1989) believed that a diagnostic feature for *Pseudoceros* is whether each vas deferens opens into the seminal vesicle separately or whether they unite to form a single duct. In *Pseudoceros* the seminal vesicle and vas deferens change shape dramatically depending on maturity. In the early stages of development of the male phase the ducts unite to open into the seminal vesicle by a common duct, but as the vesicle becomes swollen with sperm, the duct disappears and each vas deferens appears to open into the seminal vesicle separately (Figs 5A, 6).

In both genera, species were found with branching vas deferens. It is assumed that rather than being of taxonomic significance this is due to sexual maturity where fully developed vas deferens form an anastomosing network.

Seminal vesicle & ejaculatory duct. The seminal vesicle is basically elongate and oblong and there are no apparent generic or specific differences (Figs 5, 6, 7A). The walls are thick and muscular (circular muscle) and the development of musculature depends on sexual maturity since the walls are thinner when the seminal vesicle is swollen with sperm.

The ejaculatory duct is directed antero-dorsally and varies considerably in length and in the amount of coiling, but there is no apparent significant difference between the two genera (Fig. 6).

Prostate & prostatic duct. The prostate is free or independent (not interpolated into the seminal vesicle) and varies from oval to round. The muscular wall contains extraepithelial glands which

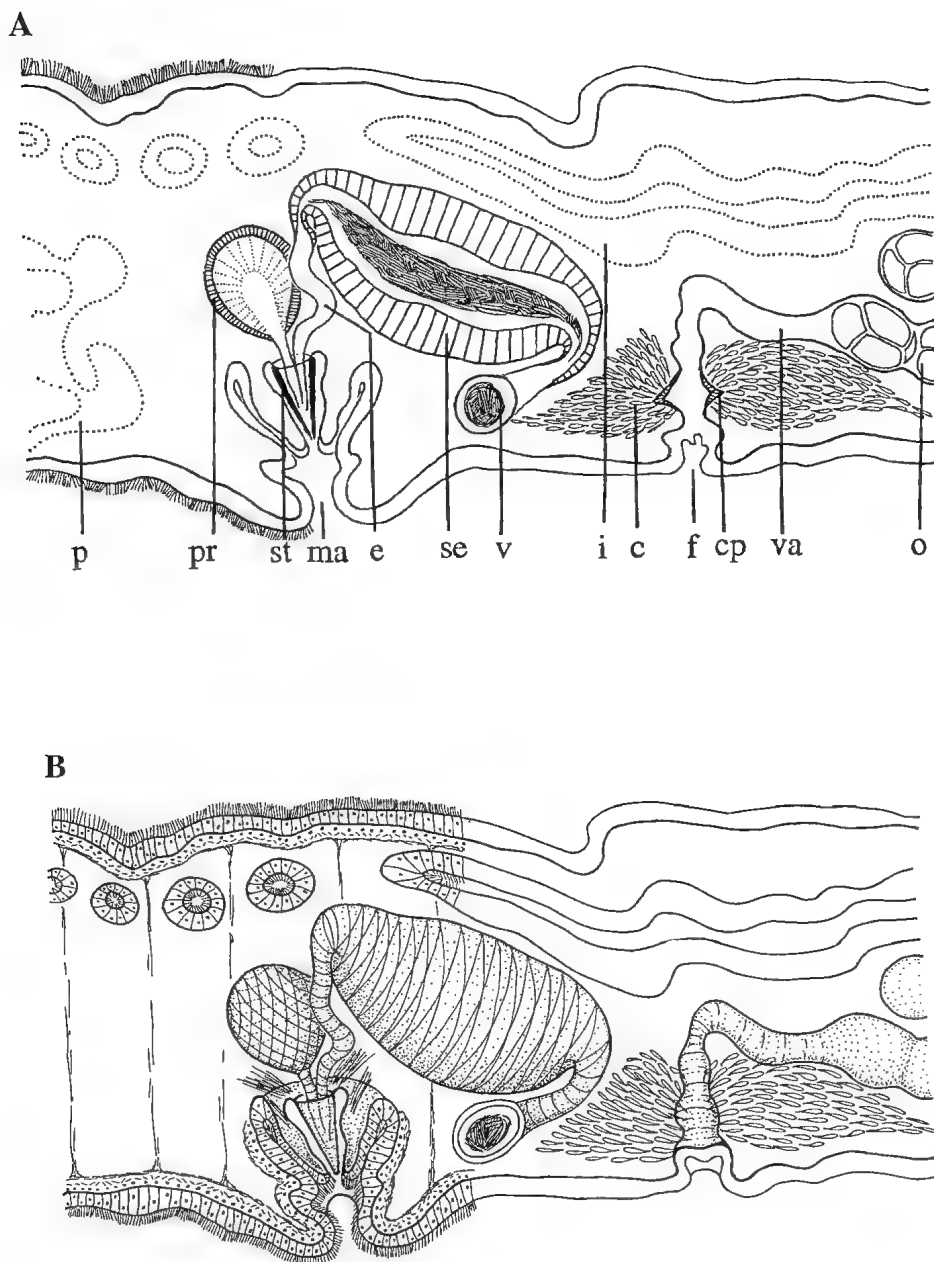


FIG. 6. Diagrammatic reconstruction of the body in the genital region showing the reproductive anatomy for *Pseudoceros* and *Pseudobiceros*. A, general distribution of organ systems; B, details of musculature. (In *Pseudobiceros*, which may be similarly diagrammatically represented, the male and female systems are not in line so they are shown separately in the descriptions).

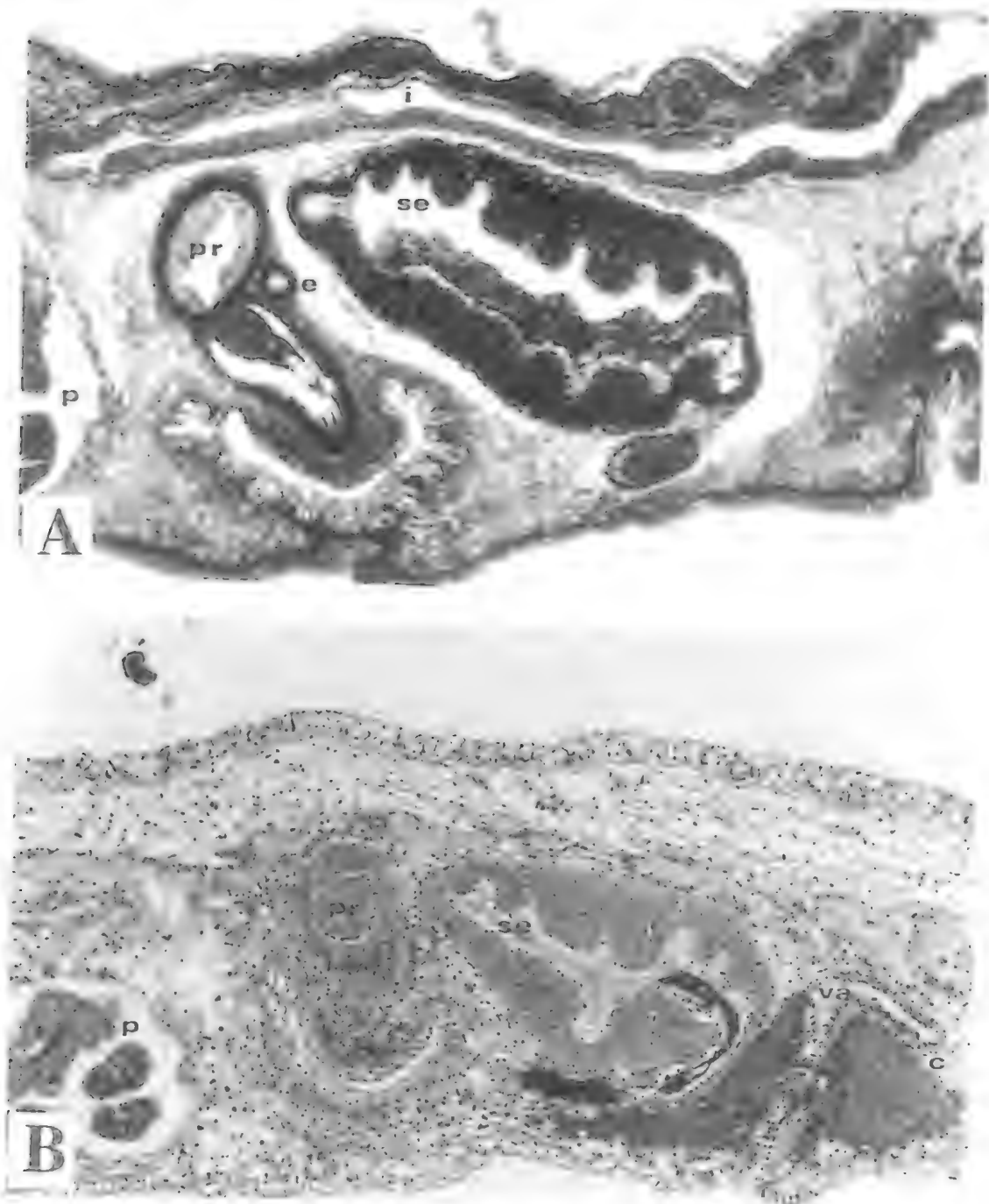


FIG. 7. Photomicrographs of the reproductive system in *Pseudoceros*. A, male; B, female.

discharge into the interior. In two large species the prostate had either an involuted lining or two separate chambers but these variations appear to be due to size. The prostatic duct is short, straight and joins the ejaculatory duct in the penis.

Penial stylet & male antrum. Although the stylet varies in width at its base, there is no apparent difference in shape between the two genera (Figs 6, 7A, 8A). The male antrum is usually wide and folded in *Pseudoceros* and deep (almost tubular) in *Pseudobiceros*. Variation in the size and shape of the penis pocket, penial sheath and antrum appear to be due to fixation, as no specific or generic differences have been determined.

Ovaries. The ovaries are scattered dorsally and extend anteriorly to the mid-pharynx region and posteriorly to the posterior margin in *Pseudoceros*, but only to the posterior end of the intestine in *Pseudobiceros* (Fig. 4).

Oviducts & vagina. The distal oviducts anastomose postero-laterally along the intestine and extend to about 1/3 the body length when the animal is fully mature, finally joining the short posteriorly directed muscular vagina (Figs 4, 5, 6). The anatomy of the female system appears to be similar between species and genera as no notable differences have been found.

Cement glands & female antrum. The cement (or 'shell') glands extend outward from the lining of the cement pouch which is located within the folded female antrum. These glands are compressed dorso-ventrally and appear to be relatively more extensive in *Pseudoceros* than in *Pseudobiceros*.

Musculature. In *Pseudoceros* the body has a thin circular muscle layer, a weak diagonal muscle layer and a more prominent longitudinal muscle layer (Fig. 6B). In *Pseudobiceros* there is an extra, though not well-defined, longitudinal muscle layer directly beneath the basement membrane. Dorso-ventral muscles are more prominent in the larger *Pseudobiceros*.

In both genera, the prostate is surrounded by crossed longitudinal muscle bands which lie over weak circular muscles (Fig. 6B). The seminal vesicle has distinct crossed circular muscle bands. There are several retractor muscles around the base of the penis sheath and there appear to be slightly more of these muscles in *Pseudobiceros*. The vagina has only weak, occasional, circular muscle bands.

Size and state of fixation appeared to contribute to slight variations observed in these patterns. No specific differences were found in the muscle

layers of the copulatory organs or in the body wall of the reproductive region.

Pseudoceros Lang, 1884

Proceros velutinus Blanchard, 1847; type unknown, painting only?

TYPE LOCALITY

Genoa, Italy.

EMENDED DIAGNOSIS

Flamboyantly or cryptically coloured. Body soft, oval, flat medially, few marginal ruffles, blunt or tapering slightly posteriorly (Fig. 2A). Pseudotentacles simple folds or broad flaps formed from the anterior margin (Fig. 3A, B). Cerebral eyespot horseshoe shaped with 20 to 60 eyes in semicircular rows, usually in an inverted heart shaped clear area. Dorsal pseudotentacular eyes in two to three scattered lines; ventral pseudotentacular eyes more numerous, extending medially to the pseudotentacular tips in two loose clusters (Fig. 3E). Pharynx anterior with about seven (one anterior, four lateral and two posterior) highly ruffled, deep, complex pharyngeal folds (Figs 4A, 5A). Intestine narrow, extends towards the posterior margin, numerous lateral branches. One male pore posterior to pharynx, between last pair of pharyngeal lobes. Female pore well separated from male pore, equidistant from it and sucker. Sucker distinct, mid-body. Male copulatory apparatus single with seminal vesicle and armed penis papilla, prostate orientated antero-dorsally.

TAXONOMIC REMARKS

Lang (1884) first described the genus *Pseudoceros* as pseudocerotids with sharp or blunt (acute or rounded) marginal pseudotentacles, without dorsal papillae, with single or double male copulatory organs and no anal pores (pores from the gut branches) dorsally.

Faubel (1984) diagnosed *Pseudoceros* as 'Pseudocerotidae with smooth dorsal surface, tentacular and cerebral eyespots present, male copulatory apparatus single with seminal vesicle and armed penis papillae, prostatic vesicle orientated antero-dorsally'. Prudhoe (1985, 1989) added that the pharynx has four or five pairs of lateral folds and that the male copulatory complex may be single or double; in the latter case they are arranged symmetrically.

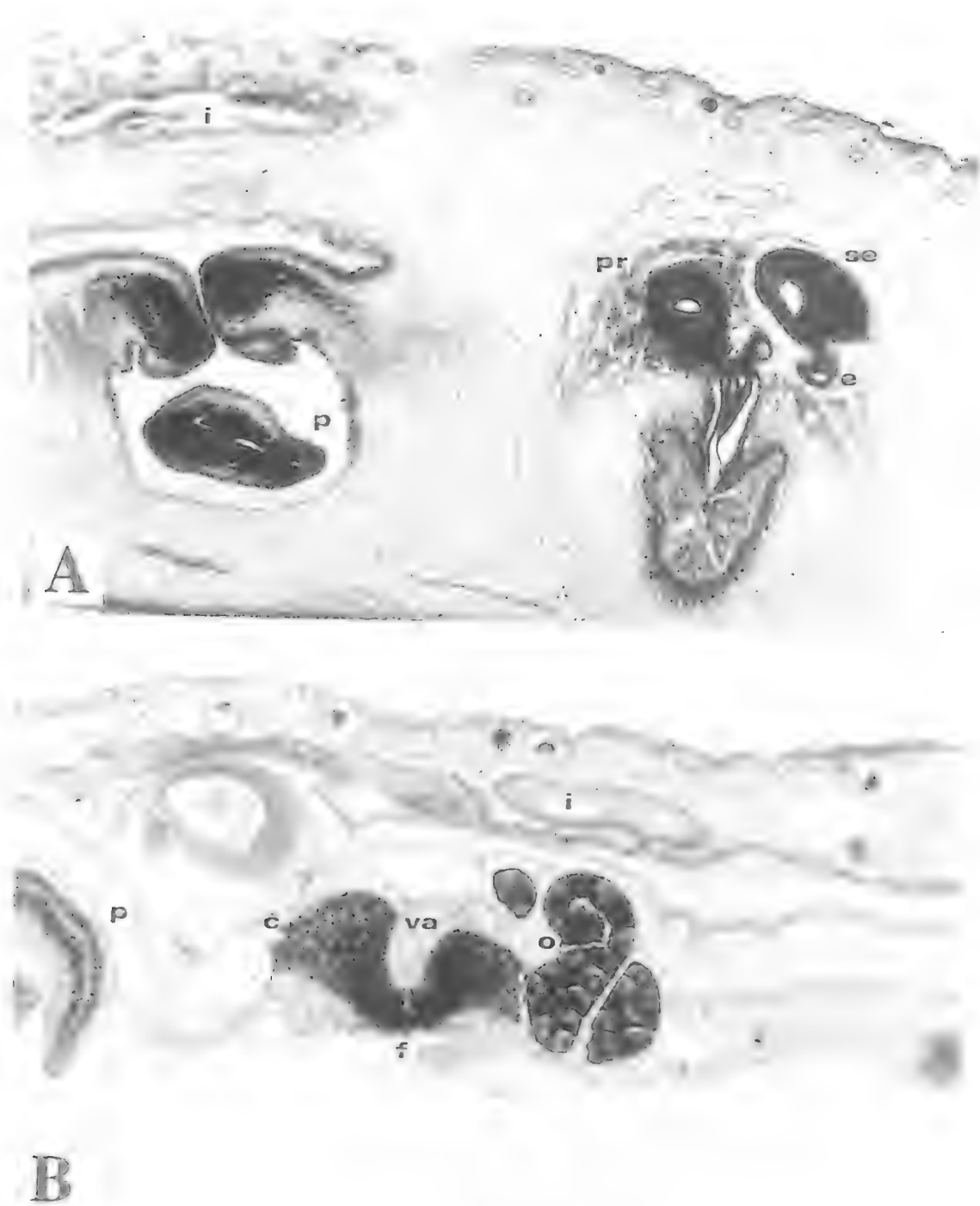


FIG. 8. Photomicrographs of the reproductive system in *Pseudobiceros*. A, male; B, female.

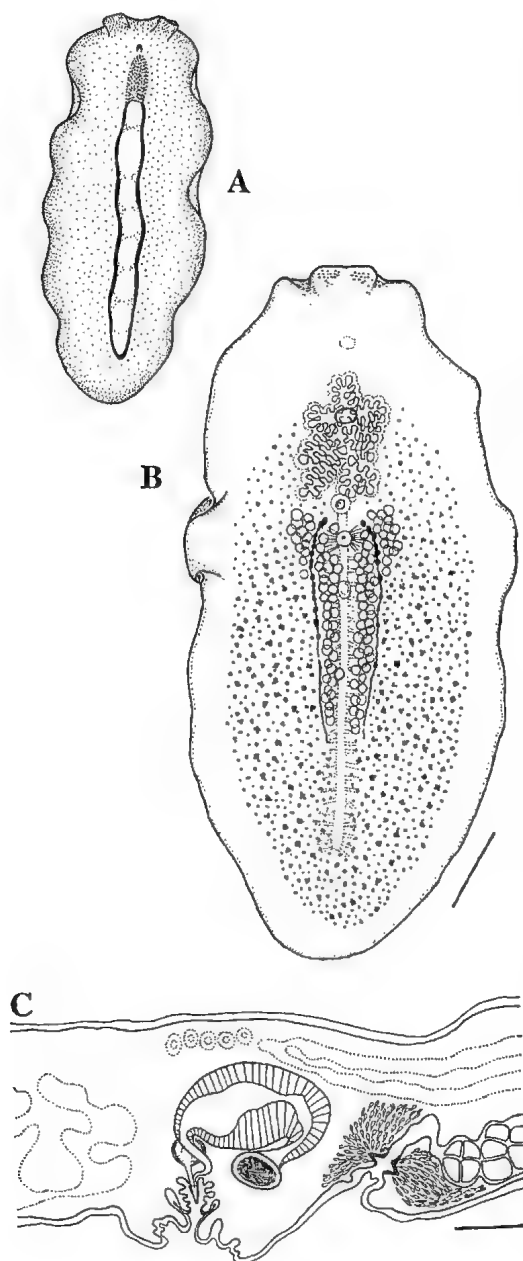


FIG. 9. *Pseudoceros bifurcus* Prudhoe, 1989. A, diagram of the dorsal colour pattern; B, QMG210332, wholemount showing the morphology from the ventral surface; C, QMG210323, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 500µm.

LIST OF RECOGNISED SPECIES

The following 26 known species we believe may be reliably placed in *Pseudoceros* sensu

stricto based on the morphology of the pharynx, eyes, pseudotentacles or reproductive anatomy (Table 1): *atropurpeus* Kato, 1939; *bifasciatus* Prudhoe, 1989; *bifurcus* Prudhoe, 1989*; *bimarginatus* Meixner, 1907*; *concinus* (Collingwood, 1876); *dimidiatus* von Graff, 1893*; *ferrugineus* Hyman, 1959*; *fuscogriseus* Hyman, 1959; *gamblei* Laidlaw, 1902; *glaucus* Prudhoe, 1989; *gravieri* Meixner, 1907*; *interruptus* (Stimpson, 1855); *kelaartii* (Collingwood, 1876); *langemaakensis* Faubel, 1984; *leptostictus* Bock, 1913*; *litoralis* Bock, 1913; *memoralis* Kato, 1938; *mossambicus* Prudhoe, 1989; *pardalis* Verrill, 1900; *perviolaceus* (Schmarda, 1859); *pius* Kato, 1944; *tomiokaensis* Kato, 1938; *tristriatus* Hyman, 1959a; *vinosus* Meixner, 1907; *violaceus* (Kelaart, 1858); *zebra* (Leuckart, 1928) (*collected during this study).

SPECIES FROM EASTERN AUSTRALIA & PAPUA NEW GUINEA

Pseudoceros bifurcus Prudhoe, 1989 (Figs 9A - C; 46A)

Pseudoceros dimidiatus von Graff, 1893; George & George, 1979: 43, pl. 49 fig. 7.

Pseudoceros unidentified species; Stummer-Traunfels, 1933: pl. 1, fig. 17.

P. liparus Marcus, 1950; Coleman, 1990: 30.

Pseudoceros bifurcus Prudhoe, 1989: 78, fig. 20.

MATERIAL EXAMINED

HOLOTYPE: Mayotte, Comoros Islands, Madagascar, 38m, P. Bouchet, 29.03.77, WM, BMNH1984.10.6.7-8.

PARATYPE: same data as holotype.

OTHER MATERIAL: Heron Is., reef slope, 3 to 15m, 12.07.89, WM, QMG210320; 12.90, WM, QMG210323; 18.02.91, S, QMG210439; 11.06.91, WM, QMG210325; WM, QMG210326; S, QMG210365; 20.06.91, LS, QMG210321; S, 4 spec., QMG210322; LS, QMG210330; 26.06.91, S, 3 spec., QMG210331; 06.91, LS, QMG210327; WM, QMG210328; 02.02.92, WM, QMG210329; 13.02.92, LS, QMG210332; 23.02.92, S, 7 spec. QMG210336; J. Tanner, 28.08.92, LS, QMG210333; 09.92, WM & LS, QMG210335; One Tree Is., reef slope, 18m, 12.09.02, LS, QMG210334. Records: Broadhurst Reef, central GBR, 15m, I. Loch, 14.10.73, CT.

DESCRIPTION

Colour & pattern. Background varies from blue (279) to light mauve (250) (cream in the largest animals) intensifying to purple (252) at the margin; lacks distinct marginal band. Pseudotentacles mauve. Bright orange (1655) regular elongate spot posterior from the cerebral eyespot

fading into an irregularly shaped white median stripe which ends before the posterior margin; stripe bordered by dark burgundy (221). Ventrally light mauve or cream, marginal band mauve.

External features. Pseudotentacles simple folds. Cerebral eyespot with about 30 eyes, occasionally with a few scattered precerebral eyes. Size: mature from 23 × 10mm to 60 × 35mm; juveniles from 1.0 × 0.4mm.

Reproductive anatomy. Seminal vesicle rounded oblong (888µm long); ejaculatory duct short, coiled. Prostatic vesicle round (185µm wide). Stylet short (130µm long). Male antrum moderately deep and voluminous. Female antrum shallow.

REMARKS

This species belongs to Group 3 where the majority of species possess a dark purple or black background. Only *P. gravieri* (Table 1) and *P. tristriatus* have a similar background colour but *P. bifurcus* has one white medial stripe not multiple yellow or orange longitudinal stripes.

Prudhoe (1989) described this species from two immature specimens and based his diagnosis on the colour pattern observed from a colour transparency (not located). Specimens from Heron Is. are identical in colour pattern to Prudhoe's description with the exception of a white marginal band. This band may be an artefact resulting from the lighter ventral surface exposed due to ruffling of the margin. Although the pharynx was not described by Prudhoe, the holotype and paratype possess complex pharyngeal folds. The reproductive anatomy was not examined by Prudhoe (1989).

Stummer-Traunfels (1933) may have first figured this species from Indonesia but it was not named. In the colour plate the animal is shown as blue with an orange median stripe bordered by black. This pattern is similar to *P. bifurcus* with the exception that the median stripe is only orange anteriorly in *P. bifurcus*.

BIOLOGY

Animals were commonly observed feeding during the day on ascidians especially *Eudistoma laysani* (Sluiter, 1900), under ledges on the reef slope. Animals were also observed copulating in situ and in the laboratory.

HABITAT & DISTRIBUTION

Found under ledges (usually on ascidian prey) on reef slope. Abundant from Heron Is., rare from One Tree Is. Records: Central GBR, Madagascar.

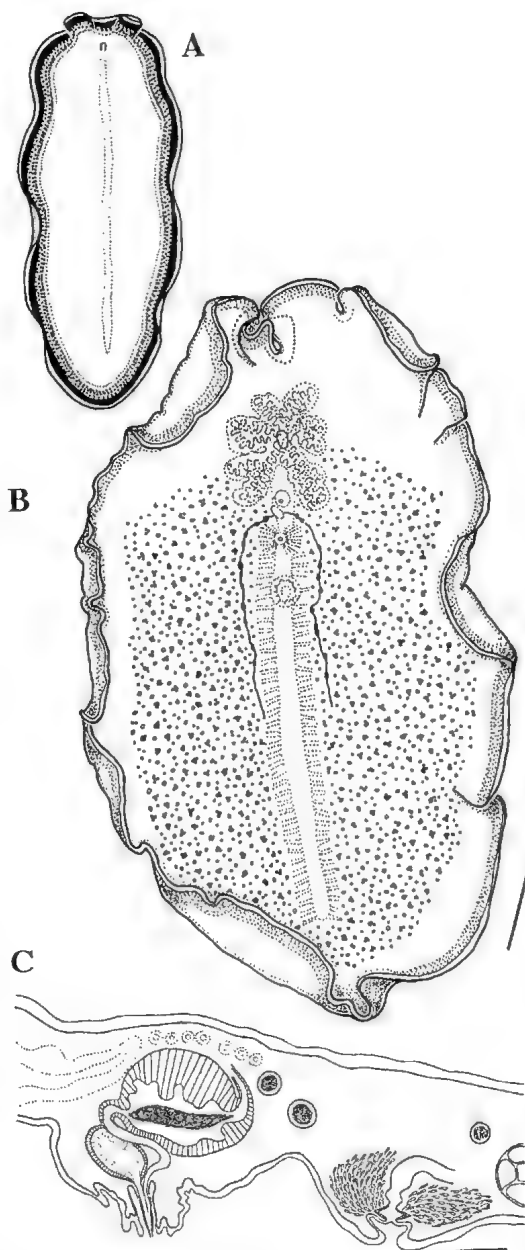


FIG. 10. *Pseudoceros bimarginatus* Meixner, 1907. A, diagram of the dorsal colour pattern; B, QMG210374, wholemount showing the morphology from the ventral surface; C, QMG210375, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 250µm.

***Pseudoceros bimarginatus* Meixner, 1907**
(Figs 10A - C; 46B)

Pseudoceros bimarginatum Meixner, 1907: 465 - 468, pl. XXV figs 5, 6; pl. XXVI, figs 17, 18; Marcus,

1950: 84; Prudhoe, 1985: 194; Prudhoe, 1989: 78 - 79.

Pseudoceros - undescribed species Stummer-Traunfels, 1933: pl. 7.

Pseudoceros corallophilus Hyman, 1954: 223, fig. 2; Faubel, 1984: 207; Coleman 1990: 31; Cannon & Newman, 1993: 83, pl. 4.

MATERIAL EXAMINED

HOLOTYPE: Unknown, Somalia.

OTHER MATERIAL: Heron Is., reef crest, 17.08.89, WM, QMG210372; 11.06.91, WM, QMG210374; 31.01.92, LS, QMG210375; 21.02.92, S, QMG210377; 10.08.92, S, QMG210381; 14.08.92, WM, QMG210382; 09.09.92, LS, QMG210383. Records: Anilao, Philippines, Stn. 13, 31.03.93, T. Gosliner, CT.

DESCRIPTION

Colour & pattern. Background white or white-cream (sometimes faint purple anteriorly) with three distinct marginal bands; inner wide orange (151), middle opaque black, narrow bright yellow-green (102) rim. Fine narrow, median white line (sometimes faint or absent), not extending to the posterior margin and along the inside of the orange marginal band. Ventrally vibrant pink-orange (135) with the same marginal bands.

External features. Pseudotentacles simple folds. Cerebral eyespot with 30 to 40 eyes. Marginal eyes obscured due to black pigmentation of the marginal band. Size: mature from 23 × 12mm to 32 × 18mm; juvenile from 12 × 6mm.

Reproductive anatomy. Seminal vesicle round (638µm long), ejaculatory duct long, coiled; vas deferens dorsally directed. Prostate small, oval (323µm wide). Stylet short (187µm long). Male and female antra wide.

REMARKS

This species belongs in Group 2. Only one other species is white, *P. gamblei*. *P. bimarginatus* has three distinct marginal bands not one as in *P. gamblei*. *P. heronensis* sp. nov. (Group 4) also somewhat resembles this species (see below).

Meixner (1907) described and illustrated this species from Gravier's original description which is as follows, 'Face dorsale rose pâle, face ventrale, même teinte, plus foncée. Sur le poutour bandes jaune d'or, brune, avec un liseré vert.' Although this colour description of the marginal bands differs slightly from ours, it is difficult to know whether the original description was based on a living or preserved animal. From the original description the relative width of the marginal bands and deeper

colour of the ventral surface convince us of the similarity in these animals.

Subsequently, Stummer-Traunfels (1933) figured this same species in a colour plate yet it remained unnamed. Hyman (1954) obviously overlooked this species when describing *P. corallophilus* 'with some hesitation' based on one preserved immature specimen from Heron Island.

The dorsally directed vas deferens and round seminal vesicle are unusual for the genus.

BIOLOGY

The vibrant orange, black and yellow marginal bands suggest that this species is displaying aposematic or warning colouration.

HABITAT & DISTRIBUTION

Found moving across boulders or sand during the day at the reef crest. Common from Heron Is. Records: Central GBR, Somalia, Philippines.

Pseudoceros bolool sp. nov.

(Figs 11A - C; 46C)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 28.12.90, WM, QMG210386.

PARATYPE: Heron Is., reef crest, 06.09.92, LS, QMG210395.

OTHER MATERIAL: Heron Is., reef crest, 29.08.89, S, 2 spec., QMG210384; 17.10.89, LS, QMG210385; 06.11.90, S, QMG210441; 02.01.91, S, QMG210387; 19.01.92, S, QMG210399; 27.01.92, LS, QMG210389; 04.02.92, S, QMG210390; 19.02.92, LS, QMG210391; WM, QMG210487; 24.08.92, LS, QMG210394; 18.02.93, S, QMG210396; 21.02.93, S, QMG210397; One Tree Is., reef crest, 19.08.93, WM, QMG210630; Madang, reef crest, 2 - 3m, 08.06.92, WM, QMG210392; 16.06.92, LS, QMG210393.

DESCRIPTION

Colour & pattern. Background velvety black, no markings, grey when extended or dark brown if gut diverticula full of food. Ventrally light grey medially, darker marginally.

External features. Pseudotentacles simple folds. Cerebral eyespot with about 60 eyes in clear area. Size: mature from 16 × 9mm to 45 × 22mm; immature from 6 × 3mm.

Reproductive anatomy. Seminal vesicle elongate, oblong (638µm long), ejaculatory duct coiled. Prostate round (203µm wide). Stylet short (113mm long). Male antrum wide.

DIAGNOSIS

Even black dorsally, with no other markings.

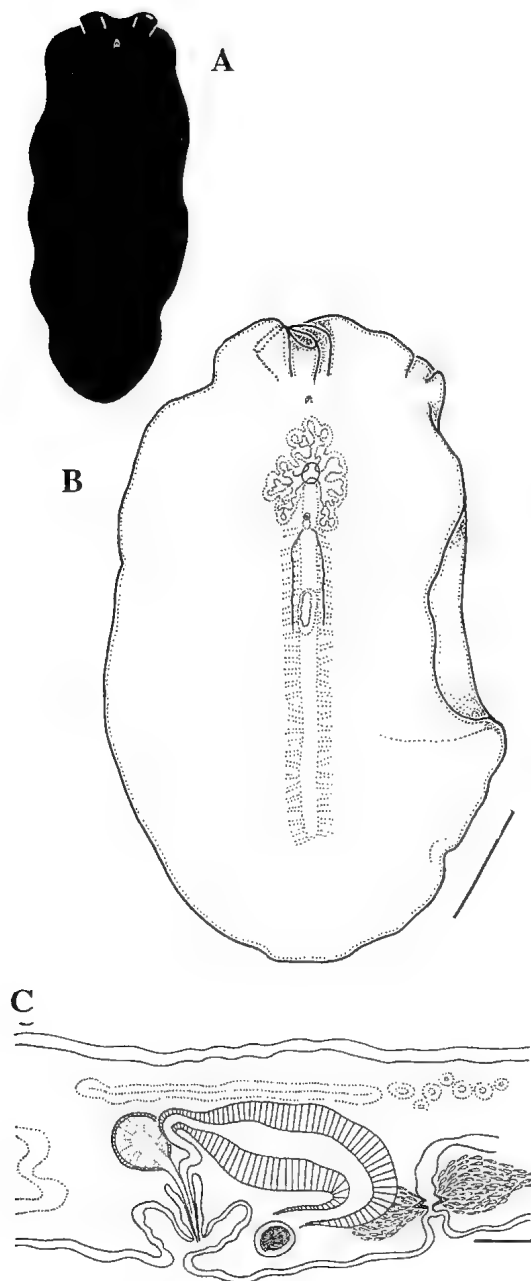


FIG. 11. *Pseudoceros bolool* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210386, wholemount showing the morphology from the ventral surface; C, QMG210395, reconstruction of the reproductive anatomy. Scales: B, 2mm; C, 250 μ m.

ETYMOLOGY

From an Australian aboriginal word for night 'bolool'.

REMARKS

This species belongs in Group 1 with the violet coloured *P. periviolaceus*.

Hyman (1959a) described *Pseudoceros ater* from Palau as uniform dark greyish or practically black without any markings. Examination of the holotype of *P. ater* (USNM28655) showed that the pharynx had simple rather than complex pharyngeal folds and may be referable to *Pseudobiceros*.

Both *P. bolool* and the nudibranch *Dendrodoris nigra* (Stimpson, 1855) are evenly black, of similar size and are often found under the same boulders. These animals are possible mimics.

HABITAT & DISTRIBUTION

Usually found on colourless, transparent, encrusting colonial ascidians under boulders at the reef crest or from under rubble on the reef slope. Common (especially juveniles) from Heron Is., rare from One Tree Is. and Madang.

Pseudoceros depiliktubub sp. nov. (Figs 12A - C; 46D)

MATERIAL EXAMINED

HOLOTYPE: Madang, reef crest, under rubble, 4m, 24.06.92, WM, QMG210473.

PARATYPE: Madang, reef crest, under rubble, 3m, 26.06.92, LS, QMG210474.

DESCRIPTION

Colour & pattern. Background velvety black fading into three marginal bands; inner marginal band black-green (556) fading to yellow-cream (127) with distinct bright orange (109) rim. Ventrally purple-black, same marginal bands.

External features. Pseudotentacles simple folds. Body sometimes with few deep marginal ruffles, tapering slightly posteriorly. Cerebral eyespot with about 30 eyes. Size: mature from 25 \times 11mm; juvenile from 20 \times 6mm.

Reproductive system. Seminal vesicle elongate oblong (795 μ m long), ejaculatory duct coiled. Prostate round (285 μ m wide). Stylet short (195 μ m long). Male antrum deep, female antrum shallow.

DIAGNOSIS

Dark green with three marginal bands; inner wide, dark green; middle wide cream; and narrow orange at rim.

ETYMOLOGY

From the Rewo Village language (Madang, PNG) name of the reef where it was collected.

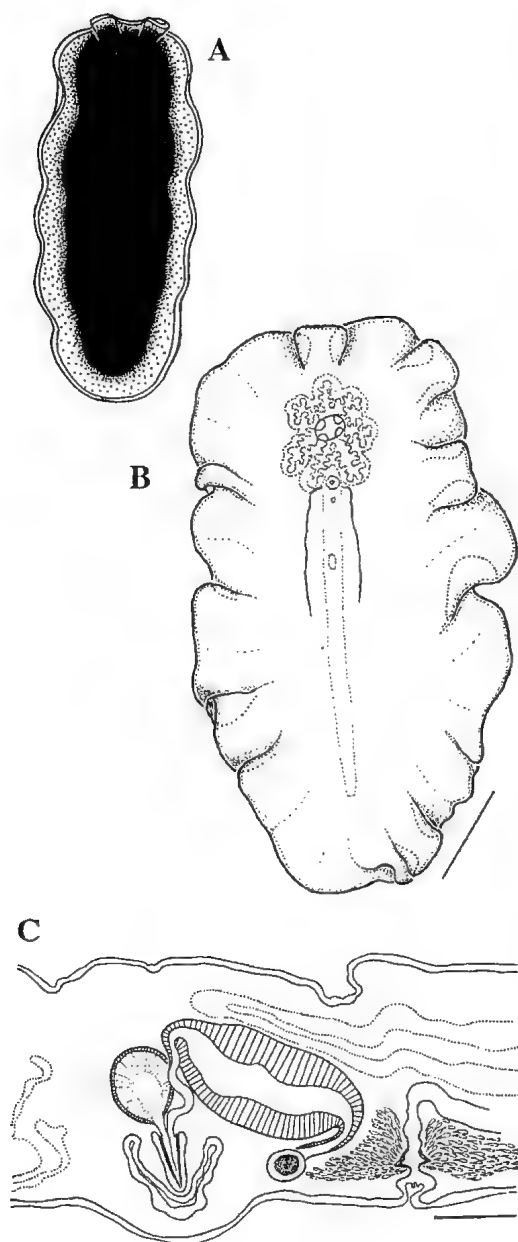


FIG. 12. *Pseudoceros depiliktub* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210473, wholemound showing the morphology from the ventral surface; C, QMG210474, reconstruction of the reproductive anatomy. Scales B, 2.5mm; C, 250 μ m.

REMARKS

This species belongs to Group 2 in which several species possess a black background with

vibrantly coloured marginal bands. *P. bimariginatus* also possesses three marginal bands, however, the bands are orange, black and yellow not green, cream and yellow as in *P. depiliktub*.

HABITAT & DISTRIBUTION

Found under rubble at the reef crest. Rare from Madang.

***Pseudoceros dimidiatus* von Graff, 1893**
(Figs 13A - C; 46E, F)

Pseudoceros dimidiatus von Graff, 1893: 362, pl. VIII;

Faubel, 1984: 238, incerta sedis.

unidentified flatworm; Steene, 1990: 322, pl. 184.

MATERIAL EXAMINED

HOLOTYPE: Painting only, GBR, Australia.

OTHER MATERIAL: Madang, reef slope, 10m, M. Ghiselin, 03.06.92, LS, G210489. Records: Wistari Reef, off Heron Is., reef slope, 20m, R. Riechelt, 16.11.80, CT; north Sulawesi, M. Severns, CT.

DESCRIPTION

Colour & pattern. Background velvety black with two median yellow (Process Yellow) stripes which vary from narrow to extremely wide, stripes begin at the pseudotentacles and continue posteriorly to join just prior to the posterior margin. Narrow black median stripe. Distinct wide orange (021) marginal band. Ventrally grey-black with orange marginal band.

External features. Large species with several deep marginal ruffles. Pseudotentacles simple folds (Fig. 46E) or broad flaps (Fig. 46F). Cerebral eyespot with 100's of eyes. Size: mature at 70 \times 25mm.

Reproductive anatomy. Seminal vesicle large (2.36mm long); ejaculatory duct short, coiled. Prostate oval (473 μ m wide) with numerous chambers resulting from an involuted lining. Stylet relatively long (225mm). Male antrum wide, female antrum narrow and shallow.

REMARKS

This species belongs in Group 3. Its flamboyant colour pattern of black with yellow longitudinal stripes and orange margin is distinct. *P. dimidiatus* is somewhat similar to *P. violaceus* which is purple with a yellow stripe and marginal band, however, the former species has two wide yellow median stripes and a distinct bright orange margin. It is surprising that this large conspicuous species has rarely been recorded since 1893. The unusual prostate with its involuted lining may be due to this species' large size.

HABITAT & DISTRIBUTION

Found under rubble from the reef slope. Rare from Madang. Record: Heron Is., N. Sulawesi.

***Pseudoceros felis* sp. nov.**
(Figs 14A - C; 46G)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 07.02.92, WM, QMG210449.

PARATYPE: Heron Is., reef crest, 21.01.92, LS, QMG210448.

DESCRIPTION

Colour & pattern. Background grey with an intricate reticulate pattern of cream, pale yellow and dark brown blotches medially; irregular black spots medially, black blotches laterally. Narrow black bifurcating stripes extending laterally to the margin, interrupted occasionally. Margin indistinct, orange (136) with an extremely narrow black rim. Ventral surface grey medially, brown laterally and orange marginally.

External features. Small species. Pseudotentacles simple folds. Cerebral eyespot with about 30 eyes. Size: mature from 20 × 15mm; juvenile from 16 × 6mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle rounded oblong (645µm long), ejaculatory duct coiled. Prostate oval (255µm wide). Stylet short (143µm long). Male and female antra shallow.

DIAGNOSIS

With narrow, transverse, bifurcating black stripes; brown and cream mottling, faint orange margin.

ETYMOLOGY

From the Latin *felis* = cat, for its wildcat-like colour pattern.

REMARKS

This species belongs in Group 6 with one other species, *P. zebra*. *P. felis* differs from *P. zebra* in possessing narrow, transverse, bifurcating stripes and distinct mottling not a few broad stripes without mottling. This colour pattern is cryptic.

HABITAT & DISTRIBUTION

Found on the topside of algal covered boulders at the reef crest. Rare from Heron Is.

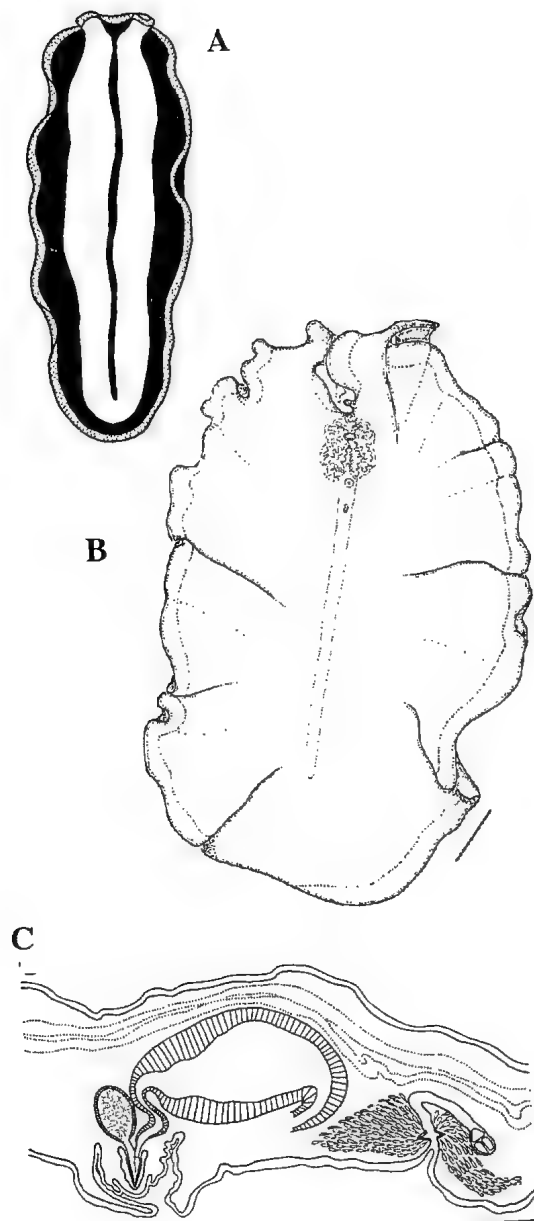


FIG. 13. *Pseudoceros dimidiatus* von Graff, in Saville-Kent, 1893. A, diagram of the dorsal colour pattern; B, QMG210489, wholemount showing the morphology from the ventral surface; C, QMG210489, reconstruction of the reproductive anatomy. Scales: B, 5mm; C, 500µm.

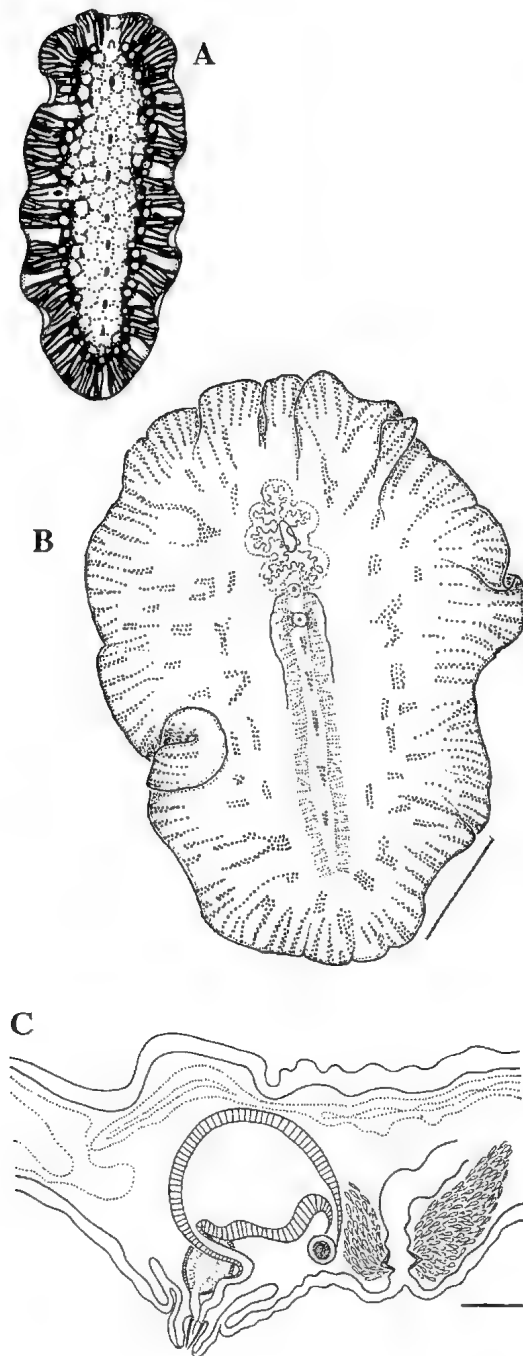


FIG. 14. *Pseudoceros felis* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210449, wholemount showing the morphology from the ventral surface; C, QMG210448, reconstruction of the reproductive anatomy. Scales: B, 2mm; C, 250 μ m.

***Pseudoceros ferrugineus* Hyman, 1959**
(Figs 15A - C; 47A)

Pseudoceros ferrugineus Hyman, 1959a: 571, fig. 9 b,c; Prudhoe, 1977: 586; Cannon & Newman, 1993: 83, pl. 4.

Pseudobiceros ferrugineus Faubel, 1984: 216.

Pseudoceros kentii von Graff, 1893: 362, pl. XIII, fig. 1; Poulter, 1987: 48, pl. 2.1.3.a.

MATERIAL EXAMINED

HOLOTYPE: Palau, Micronesia, Stanford Team, 20.10.55, S, USNM 28652.

OTHER MATERIAL: Heron Is., reef crest, 31.07.89, WM + eggs, QMG21036; WM, QMG210486; 17.10.89, LS & WM, QMG210365; WM, QMG210366; 26.06.91, S, QMG210440; 07.02.92, WM, QMG219367; 19.02.92, LS, QMG210368; 03.09.92, LS, QMG210369. Records: Broadhurst Reef, central GBR, reef slope, 15m, I. Loch, 29.06.74, CT; Philippines, 31.03.93, T. Gosliner, CT.

DESCRIPTION

Colour & pattern. Background dark red (186) with many small, compacted white dots covering the entire surface (making it appear brilliant purple-pink); dots more concentrated laterally. Two distinct marginal bands; inner marginal band red without dots (varies from narrow to wide), outer band bright orange (021). Ventral surface red intensifying to burgundy (220) towards the margin. Juveniles with same pattern except the white dots are fewer and relatively larger.

External features. Large species, margin with several deep ruffles. Pseudotentacles simple folds or broad flaps. Cerebral eyespot with a very large number of eyes. Size: mature from 60 \times 35mm to 45 \times 21mm; juvenile from 6 \times 3mm.

Reproductive anatomy. Vas deferens branched. Seminal vesicle long (1.5mm), ejaculatory duct short. Prostatic vesicle small (285 μ m wide) with two chambers, highly muscular prostatic duct. Stylet small (158 μ m long). Male and female antra shallow.

REMARKS

This species belongs in Group 4 where only one other species possesses a red background, *P. vinosus*; however, *P. ferrugineus* possesses numerous, minute, white dots not white and yellow flecks.

Hyman (1959a) originally described this species as having two male pores. Examination of the holotype revealed only one male pore and complex pharyngeal folds which is characteristic

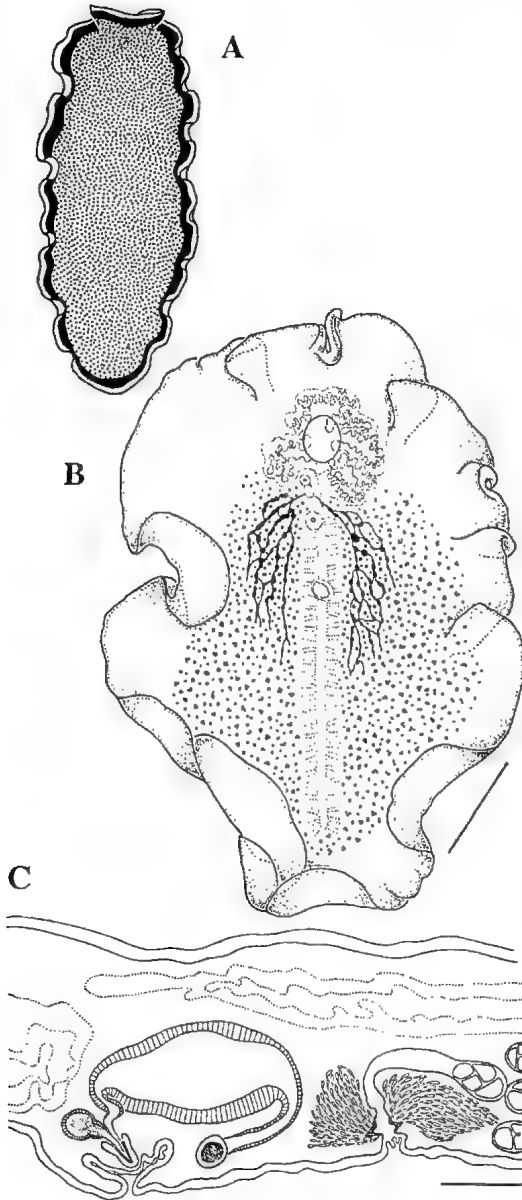


FIG. 15. *Pseudoceros ferrugineus* Hyman, 1959. A, diagram of the dorsal colour pattern; B, QMG210364, wholemount showing the morphology from the ventral surface; C, QMG210369, reconstruction of the reproductive anatomy. Scales: B, 1mm; C, 250µm.

of the genus. The two chambered prostate is unique to this species.

BIOLOGY

One animal was observed laying a thin layer of red eggs on an empty bivalve shell in an

aquarium. Similar eggmasses have also been observed when an animal was removed from colonial ascidians under boulders.

HABITAT & DISTRIBUTION

This flamboyant species is found under boulders (sometimes on pink encrusting colonial ascidians) at the reef crest. Common from Heron Is. Records: Central GBR, Micronesia, Philippines.

Pseudoceros goslineri sp. nov. (Figs 16A - C; 47B)

MATERIAL EXAMINED

HOLOTYPE: Madang, reef slope, under sponge, 30m, 19.06.92, WM, QMG210454.

PARATYPE: Madang, reef crest, 3m, T. Gosliner, 15.06.92, LS, QMG210453.

OTHER MATERIAL: Heron Is., reef crest, 04.02.92, WM, QMG210452; reef slope, 12m, 02.02.93, LS, QMG210455. One Tree Island, reef crest, 16.08.93, S, QMG210493. Other Record: Wheeler Reef, central GBR, reef slope, 12m, I. Loch, 28.07.74, CT.

DESCRIPTION

Colour & pattern. Colour pattern variable. Background cream mottled with orange, pink and brick red dots (PNG animals darker brown medially, brown not orange dots); concentrated brick red dots medially appearing as irregular elongate blotches. Margin composed of purple (240) and pink (236) irregular dots and spots, marginal spots closer together anteriorly across pseudotentacles. Ventrally light violet (263).

External features. Pseudotentacles simple folds. Cerebral eyespot with about 30 eyes. Size: mature from 70 × 28mm to 14 × 8mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle elongate (623µm long); ejaculatory duct short, coiled. Prostate round (225µm wide). Stylet extremely short (98µm long). Male and female antra deep.

DIAGNOSIS

Cream with purple, pink and orange spots; margin with purple and pink spots and dots.

ETYMOLOGY

For Dr Terry Gosliner.

REMARKS

This species belongs in Group 4 in which several species possess a cream background, however, *P. goslineri* most closely resembles *P. ouini* sp. nov.

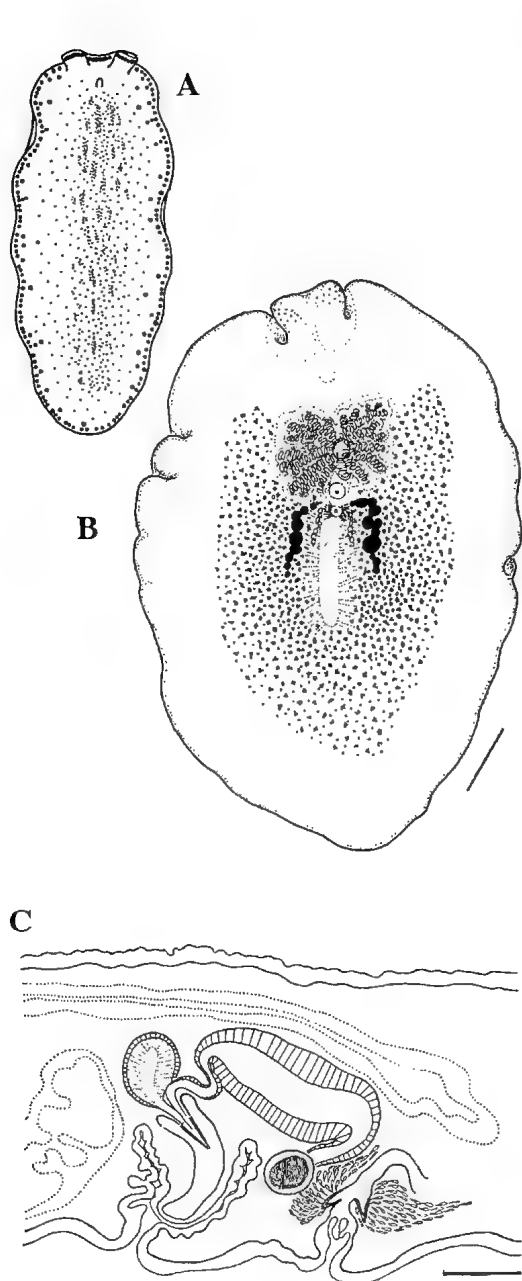


FIG. 16. *Pseudoceros goslineri* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210453, wholemound showing the morphology from the ventral surface; C, QMG210454, reconstruction of the reproductive anatomy. Scales: B, 1mm, C, 500 μ m.

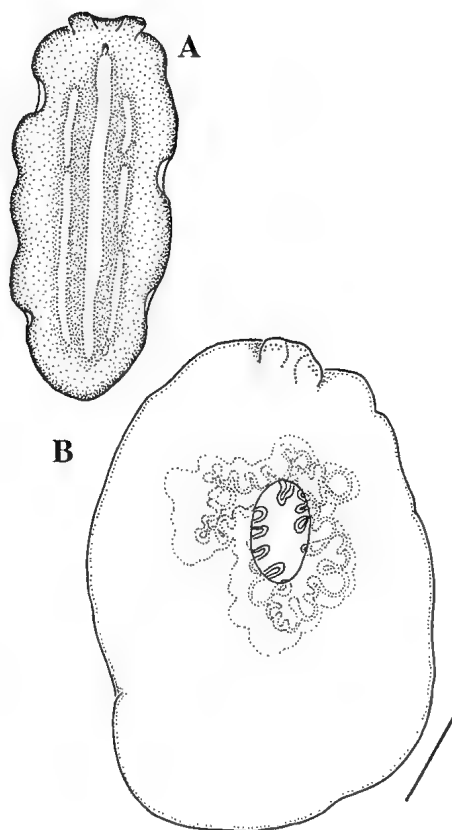


FIG. 17. *Pseudoceros gravieri* Meixner, 1907. A, diagram of the dorsal colour pattern; B, QMG210345, wholemound showing the morphology from the ventral surface. Scales: B, 2.5mm; C, 250 μ m.

HABITAT & DISTRIBUTION

Found under boulders from the reef crest to the reef slope (one animal found on a sponge at 30m). Rare from Heron, One Tree Is. and Madang. Record: Central GBR.

Pseudoceros gravieri Meixner, 1907 (Figs 17A, B; 47C, D)

Pseudoceros gravieri Meixner, 1907: 468-469, Pl. XXVI, figs 7a, 7b, 12; Prudhoe, 1989: 83.

MATERIAL EXAMINED

HOLOTYPE: Unknown, Djibouti.

OTHER MATERIAL: Heron Is., reef slope, 9m, 12.07.89, WM, QMG210345. Record: GBR, G. Allan, CT.

DESCRIPTION

Colour & pattern. Background blue-purple (279 or 2715), darker medially, intensifying to purple (252) at margin. Three bright yellow (122) longitudinal stripes in immature specimen; central stripe wide; two lateral stripes narrower, shorter and discontinuous (Fig. 47C). Larger specimens (Fig. 47D) with numerous discontinuous longitudinal yellow stripes. Ventrally light mauve.

External features. Pseudotentacles simple folds. Size: juvenile at 6×3 mm.

Reproductive anatomy. The only specimen collected was immature.

REMARKS

This species belongs in Group 3 where the majority of species possess a dark purple or black background. Only *P. gravieri*, *P. bifurcus* and *P. tristriatus* are blue as mentioned above.

According to Meixner (1907), Gravier first described this species as having, 'bandes jaune d'or encadrées par des bandes bleu foncé. Un liseré bleu plus clair sur tout le poutour'. The figure given by Meixner shows that this species possesses a complex pharynx and simple folded pseudotentacles which is characteristic of the genus.

This species could be easily confused with *P. tristriatus* Hyman, 1959a which is described as blue with three longitudinal orange stripes, each stripe bordered by black and extending almost to the posterior end. However, *P. gravieri* has a variable number of yellow longitudinal stripes that are clearly not bordered by black.

HABITAT & DISTRIBUTION

Found on blue-purple ascidians (*Clavelina* sp.) under ledges on the reef slope. Rare from Heron Is. Record: GBR, Djibouti.

***Pseudoceros heronensis* sp. nov.**
(Figs 18A - C; 47E)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 17.08.92, WM, QMG210462.

PARATYPE: Heron Is., reef crest, 08.09.92, LS, QMG210465.

OTHER MATERIAL: Heron Is., reef crest, 22.02.92, S, QMG210460; 29.07.92, LS, QMG210461; 06.09.92, WM, QMG210463; WM, QMG210464; 21.02.93, WM, QMG210466.

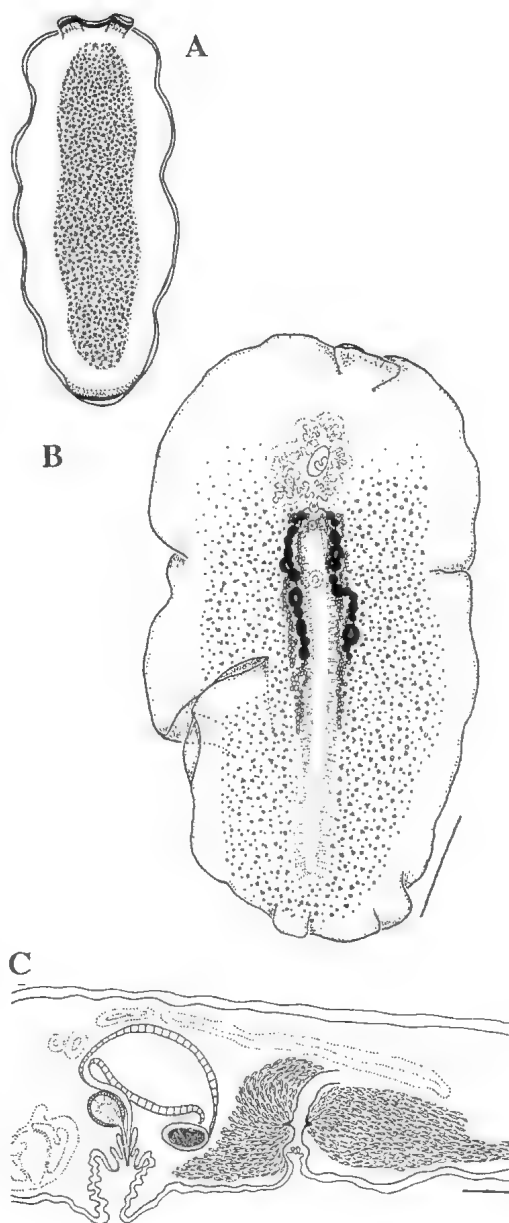


FIG. 18. *Pseudoceros heronensis* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210462, wholemount showing the morphology from the ventral surface; C, QMG210465, reconstruction of the reproductive anatomy. Scales: B, 5mm; C, 500µm.

DESCRIPTION

Colour & pattern. Background cream-yellow; medially with small chocolate brown (483) and

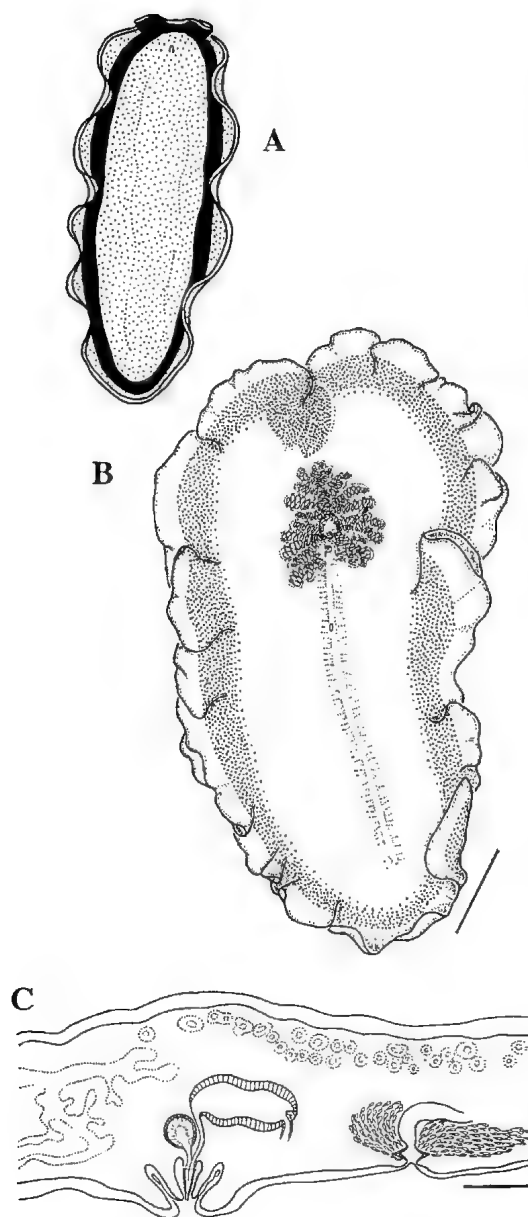


FIG. 19. *Pseudoceros jebborum* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210470, wholemount showing the morphology from the ventral surface; C, QMG210471, reconstruction of the reproductive anatomy. Scales: B, 5mm; C, 500 μ m.

white dots (clusters of microdots). Margin extremely wide, cream, covered in orange (172) microdots; narrow yellow-green (394) rim. Three narrow marginal bands found only anteriorly on pseudotentacles and along the posterior margin;

inner band orange (165), middle band black and yellow-green at rim. Gut diverticula usually orange.

External features. Small species. Pseudotentacles simple folds. Cerebral eyespot with about 20 eyes. Size: mature from 18 \times 8mm to 28 \times 12mm; juvenile from 14 \times 6mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle round oblong (600 μ m long); ejaculatory duct long, not coiled. Prostate round (188 μ m width). Stylet short (135mm long). Male antrum deep and voluminous; female antrum deep, cement glands extensive.

DIAGNOSIS

Cream with orange, black and yellow short marginal bands occurring only anteriorly along the pseudotentacles and along the posterior margin, mottled medially.

ETYMOLOGY

For the Heron Island Research Station.

REMARKS

This species belongs in Group 4 in which several other species possess a cream, yellow or white background. *P. heronensis* is somewhat similar to *P. bimarginatus* which also possesses orange, black and yellow marginal bands, however, *P. heronensis* has these marginal bands restricted to the anterior and posterior end not around the entire margin. This species also resembles *P. verecundus* sp. nov. Cryptic on colonial ascidians.

HABITAT & DISTRIBUTION

Found under boulders, usually feeding on orange and pink colonial ascidians. Common from Heron Is.

Pseudoceros jebborum sp. nov. (Figs 19A - C; 47F)

Pseudoceros sp. Poulter, 1987: 48, pl. 2.1.2.f

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef slope, 3m, 01.02.93, WM, QMG210470.

PARATYPE: Heron Is., reef slope, 10m, 06.02.93, LS, QMG210471.

OTHER MATERIAL: Madang, reef crest, 3m, 23.06.92, WM, QMG210467; 26.06.92, LS, QMG210468; 28.06.92, WM, QMG210469; Heron Is., reef slope, 10m, 06.02.93, S, QMG210472.

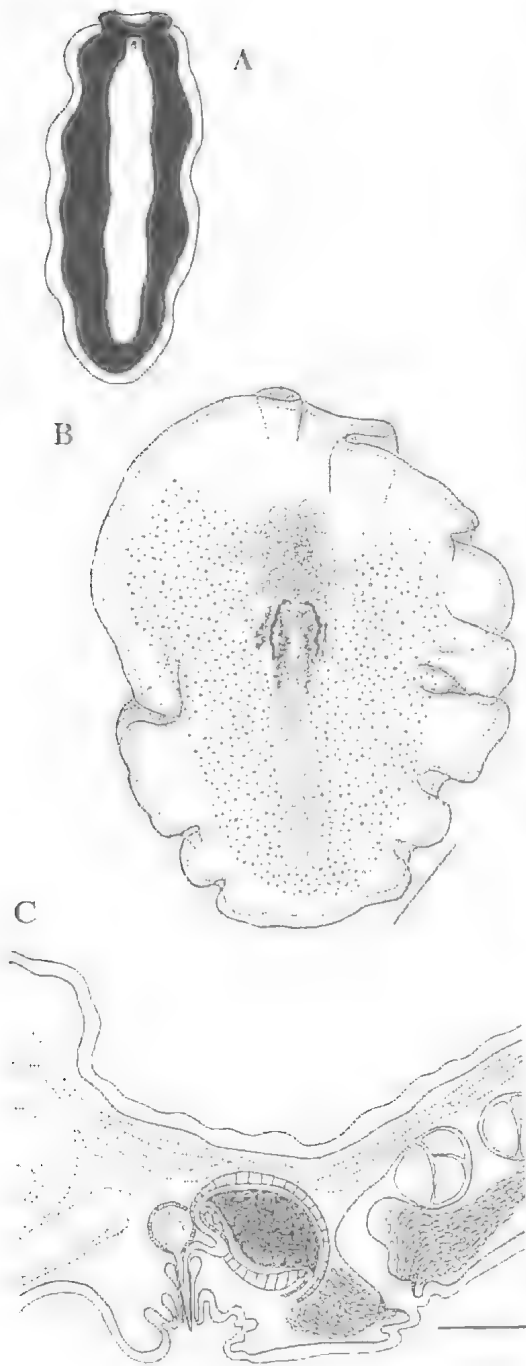


FIG. 20. *Pseudoceros laticlavus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210354, wholemount showing the morphology from the ventral surface; C, QMG210353, reconstruction of the reproductive anatomy. Scales: B, 2mm; C, 250 μ m.

DESCRIPTION

Colour & pattern. Background cream-orange (121), grey black laterally near the margin and across the pseudotentacles. Marginal band wide, cream with a narrow distinct bright yellow (102) rim. Ventrally same colour pattern, pharyngeal lobes usually dark purple.

External features. Margin with shallow ruffles, tapering slightly posteriorly. Pseudotentacles simple folds. Cerebral eyespot relatively small with about 60 eyes. Size: mature from 70 \times 30mm to 40 \times 30mm; juvenile (or not mature) from 27 \times 10mm to 70 \times 32mm.

Reproductive anatomy. Seminal vesicle long (850 μ m); ejaculatory duct short, not coiled. Prostate small, round (240 μ m wide). Stylet relatively large (278 μ m long), larger than prostate. Male and female antra shallow.

DIAGNOSIS

Cream-orange medially with two distinct marginal bands; inner wide black, outer cream-orange.

ETYMOLOGY

For the Jebb family (Christensen Research Institute, Madang).

REMARKS

This species belongs in Group 2 and is the only one possessing an orange background. *P. jebborum* somewhat resembles *P. paralaticlavus* sp. nov. (Group 3) in pattern, however, the former species has a narrow black marginal band, not a black background. Several animals were found to be immature although they were relatively large (i.e. 70 \times 32mm).

HABITAT & DISTRIBUTION

Found under rubble on the reef slope. Rare from Heron Is., Madang. Record: Hawaii.

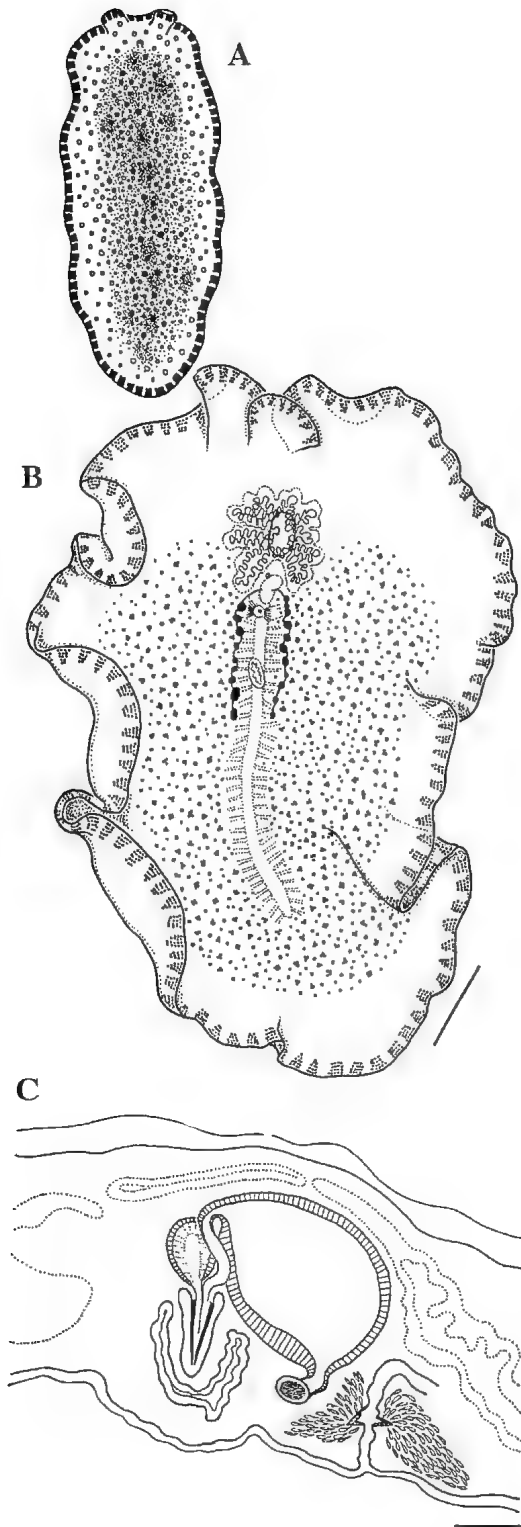
Pseudoceros laticlavus sp. nov. (Figs 20A - C; 48A)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 31.07.89, WM, QMG210346.

PARATYPES: Heron Is., reef crest, 31.07.89, WM, QMG210347; 14.02.92, LS, QMG210353; WM, QMG210348; S, QMG210349.

OTHER MATERIAL: Heron Is., reef crest, 06.11.90, S, QMG210443; 20.06.91, S, QMG210350; 21.01.92, LS, QMG21035; 31.01.92, WM, QMG210352; 19.02.92, WM, QMG210354; S, QMG210358; 26.08.92, WM, QMG210355; S, QMG210356;



31.08.92, WM, QMG210357; S, 2 spec., QMG210438; 04.02.93, WM, QMG210359; LS, QMG210360; 17.02.93, WM, QMG210361; 20.02.93, S, QMG210362; One Tree Is., reef crest, 16.08.93, QMG210492.

DESCRIPTION

Colour & pattern. Background black (not velvety) with a single wide white median stripe; marginal band wide white, discontinuous over the pseudotentacles. Ventrally same pattern.

External features. Relatively small species. Pseudotentacles simple folds. Cerebral eyespot with about 15 eyes. Size: mature from 14×8 mm to 30×10 mm; juvenile from 3×2 mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle small, rounded oval ($338\mu\text{m}$ long); ejaculatory duct coiled. Prostate extremely small ($113\mu\text{m}$ wide). Stylet narrow ($158\mu\text{m}$ long), larger than prostate. Male and female antra shallow and wide.

DIAGNOSIS

Black with a single white median stripe and wide white margin.

ETYMOLOGY

From the Latin *laticlavus* = broad stripe, referring to the distinct median stripe.

REMARKS

This species belongs in Group 3 in which several species possess a dark purple or black background but only one other species also has white stripes, *P. paralaticlavus* sp. nov.

HABITAT & DISTRIBUTION

Found on colonial ascidians, under boulders at reef crest. Common from Heron Is., rare from One Tree Is.

Pseudoceros leptostictus Bock, 1913 (Fig. 21A - C; 48B)

Pseudoceros leptostictus Bock, 1913: 256-257, pl. III, fig. 12, 13; Marcus, 1950: 86; Prudhoe, 1977: 597-598; Faubel, 1984: 239, incerta sedis.

FIG. 21. *Pseudoceros leptostictus* Bock, 1913. A, diagram of the dorsal colour pattern; B, QMG210341, wholemount showing the morphology from the ventral surface; C, QMG210342, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, $250\mu\text{m}$.

MATERIAL EXAMINED

HOLOTYPE: unknown, Western Australia.

PARATYPE: Western Australia, not located, AM W.5457.

OTHER MATERIAL: Heron Is., reef crest, 29.09.89, WM, QMG210338; reef slope, 6m, 30.02.92, LS, QMG210342; reef crest, 29.07.92, WM, QMG210341; 23.08.92, LS, QMG210343; 06.09.92, WM, QMG210344; Motupore Is., off Port Moresby, PNG, reef slope, D. Brunckhorst, 17.06.88, S, QMG210339; Madang, reef crest, 26.06.92, WM, QMG210340.

DESCRIPTION

Colour & pattern. Background cream-white: pale yellow (127) medially with orange-brown (158) blotches; entire surface covered with small scattered spots, spots orange laterally, black medially, interspersed with smaller white spots. Marginal band interrupted, narrow black with an extremely narrow, yellow-green (387) rim. Ventrally pink (211) with an uninterrupted black marginal band.

External features. Pseudotentacles simple folds. Cerebral eyespot small with about 40 eyes. Pseudotentacular eyes obscured due to black pigment. Size: mature from 16 × 9mm to 26 × 10mm; juvenile 10 × 5mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle rounded oblong (825µm long), ejaculatory duct coiled. Prostate oval (263µm wide), same size as stylet (263µm long). Male and female antra deep.

REMARKS

This species belongs in Group 4 in which four other species possess a cream background colour. Only two species have an interrupted marginal band, *P. interruptus* and *P. memorialis*. *P. leptostictus* differs from *P. interruptus* by its cream colour and narrow black and yellow-green marginal bands, not brownish with mottles of reddish brown and four marginal bands, and differs from *P. memorialis* in having two distinct marginal bands not three.

Bock (1913) originally described this species (from a preserved specimen) as sandy yellow, brighter yellow medially becoming reddish towards the margins, black stippling over the dorsal surface, margin with a band of quadrangular blackish markings, bounded by a thin band of yellow. The pharynx and the reproductive structures were not described by Bock or Prudhoe (1977) but the description of the characteristic colour pattern is similar to our specimens.

HABITAT & DISTRIBUTION

Found on purple colonial ascidians under boulders at the reef crest and under ledges on the reef slope. Rare from Heron Is., Madang and Motupore Is. (9°31' S, 147°10' E), south PNG. Records: Northern GBR, Western Australia.

***Pseudoceros lindae* sp. nov.**

(Figs 22A - C; 48C)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef slope, 10m, 23.02.93, WM, QMG210417.

PARATYPES: Heron Is., reef slope, 10m, 17.02.90, WM, QMG210413; 23.02.93, LS, QMG210416.

OTHER MATERIAL: Heron Is., reef slope, 3 - 12m, 07.10.89, WM, QMG210412; 26.06.91, WM & LS, QMG210414; 27.01.93, LS, QMG210415.

DESCRIPTION

Colour & pattern. Dramatic pattern of maculae in vivid colours. Background burgundy (214) intensifying towards the margin; numerous large golden-yellow (116) oval to round shaped maculae medially, becoming larger and blue laterally and blending into the marginal band. Background fading to turquoise (311) then sky blue (2975) towards the margin; margin composed of large turquoise and sky blue maculae which form an irregular wide band. Ventral surface light purple-violet (2635).

External features. Body thick and fleshy. Pseudotentacles broad flaps. Pharynx with highly ruffled complex pharyngeal folds. Size: mature from 32 × 12mm to 44 × 12mm; juvenile from 25 × 17mm.

Reproductive anatomy. Vas deferens branched. Seminal vesicle elongate oblong (1.5mm long); ejaculatory duct short, coiled. Prostate large oval (444µm wide). Stylet short (185µm long). Male and female antra deep.

DIAGNOSIS

Burgundy background with large golden yellow maculae medially and blue maculae marginally.

ETYMOLOGY

In honour of Mrs Linda Newman.

REMARKS

This species belongs in Group 5 with two other species. *P. lindae* differs from these species by having a burgundy background not grey background as in *P. glaucus* nor black as in *P. scintillatus* sp. nov.

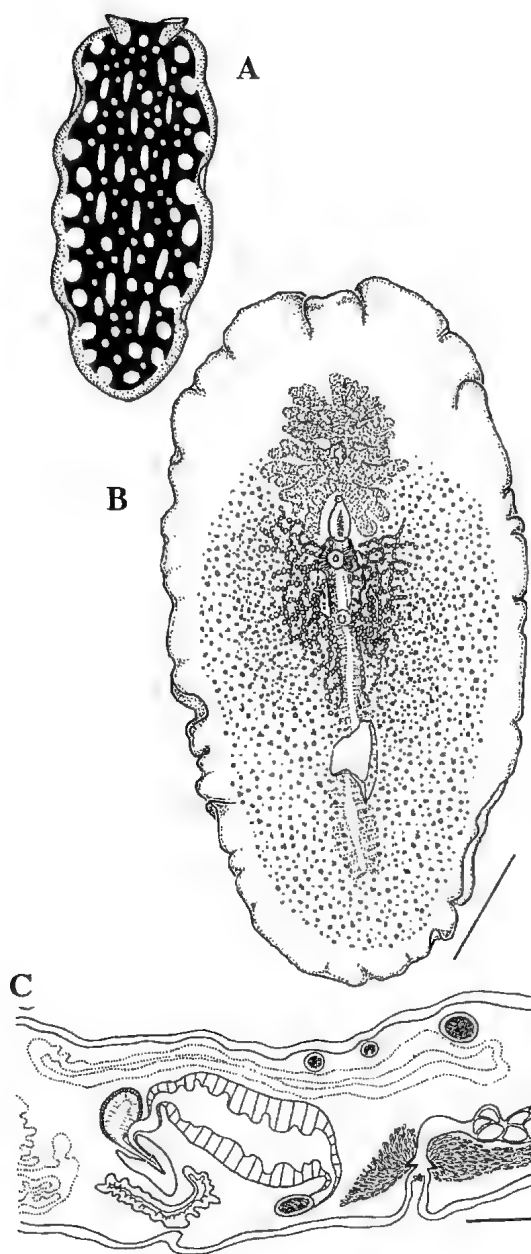


FIG. 22. *Pseudoceros lindae* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210417, wholmount showing the morphology from the ventral surface; C, QMG210416, reconstruction of the reproductive anatomy. Scales: B, 5mm; C, 500 μ m.

BIOLOGY

Animals were observed copulating in situ and in the laboratory, both animals showing damage from copulation (Fig. 48C).

HABITAT & DISTRIBUTION

This species tends to be more common under ledges on the reef slope especially at night. Common from Heron Is.

Pseudoceros monostichos sp. nov. (Figs 23A - C; 48D)

MATERIAL EXAMINED

HOLOTYPE: Madang, reef crest, 26.06.92, WM, QMG210451.

OTHER MATERIAL: Wistari Reef, off Heron Is., reef slope, 10m, 28.01.92, LS, QMG210450.

DESCRIPTION

Colour & pattern. Background cream with a distinct narrow black-brown median line; line bisects the cerebral eyespot anteriorly, does not extend to the posterior margin; line bordered laterally by white and then light brown. Narrow margin with four indistinct bands; inner band yellow (106) intensifying to green (367) then sky blue (298) then purple (257) at rim. Ventrally cream with same marginal bands, wide dark purple-black median stripe, dark grey laterally.

External features. Dorsal surface with numerous dimples only observed when resting, tapering slightly posteriorly. Pseudotentacles broad flaps. Cerebral eyespot obscured due to dark pigment of the median line. Size: mature 35 \times 12mm; juvenile 25 \times 9mm.

Reproductive anatomy. Seminal vesicle large (1.5mm long), ejaculatory duct not coiled. Prostata oval (300 μ m wide). Stylet extremely small (113 μ m long). Male and female antra shallow.

DIAGNOSIS

Cream with a single narrow dorsal median black-brown median stripe, wide brown ventral median stripe and unusual dimpled texture of the dorsal surface.

ETYMOLOGY

From the Latin *mono* = one, *stichos* = line, for its characteristic narrow median stripe.

REMARKS

This species belongs in Group 3. No other species from this group has a cream background colour. *P. bifurcus* has a wide median stripe, however, this white stripe is bordered by burgundy and is not a fine black median line as in *P. monostichos*. This species is unusual as the ventral surface is more strikingly patterned than the dorsal surface.

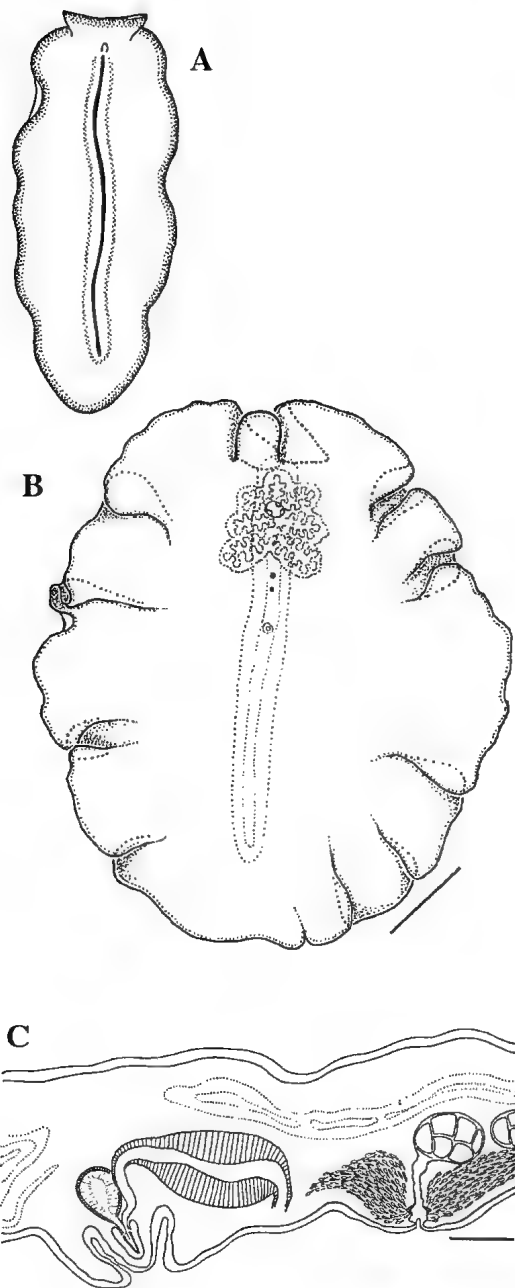


FIG. 23. *Pseudoceros monostichos* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210451, wholemount showing the morphology from the ventral surface; C, QMG210450, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 250 μ m.

HABITAT & DISTRIBUTION

Found under rubble at the reef crest and under ledges on the reef slope. Rare from Heron Is. and Madang.

Pseudoceros ouini sp. nov. (Figs 24A - C; 48E)

MATERIAL EXAMINED

HOLOTYPE: Madang, reef crest, 27.06.92, WM & LS, QMG210631.

DESCRIPTION

Colour & pattern. Background transparent beige and opaque cream-white with faint orange mottling medially and laterally. Margin with well spaced, evenly sized, bright pink (232) spots, spots more concentrated anteriorly to form a band across the pseudotentacles. Ventrally white, margin with same spotted pattern.

External features. Pseudotentacles broad flaps. Cerebral eyespot with about 30 eyes. Size: mature at 20 \times 10mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle small (638 μ m long); ejaculatory duct short, not coiled. Prostate small round (240 μ m wide). Stylet short (128 μ m long). Male and female antra deep.

DIAGNOSIS

Cream background with widely spaced, evenly sized, pink marginal spots.

ETYMOLOGY

For Mr Jean-Marc Ouin.

REMARKS

This species belongs in Group 4. Several other species possess a cream background colour, but only *P. concinnus* and *P. goslineri* have spots along the margin. *P. concinnus* (Collingwood, 1876) was originally described as 'cream coloured with an edging of blue all around, composed of small and larger spots running into one another'. The margin is distinctly different in *P. ouini* since the spots are widely spaced and pink rather than blue. *P. goslineri* is similarly coloured but the pink dots and spots along the margin are more numerous and irregular, with distinct brown blotches medially.

DISTRIBUTION

Found under rubble at the reef crest. Rare from Madang.

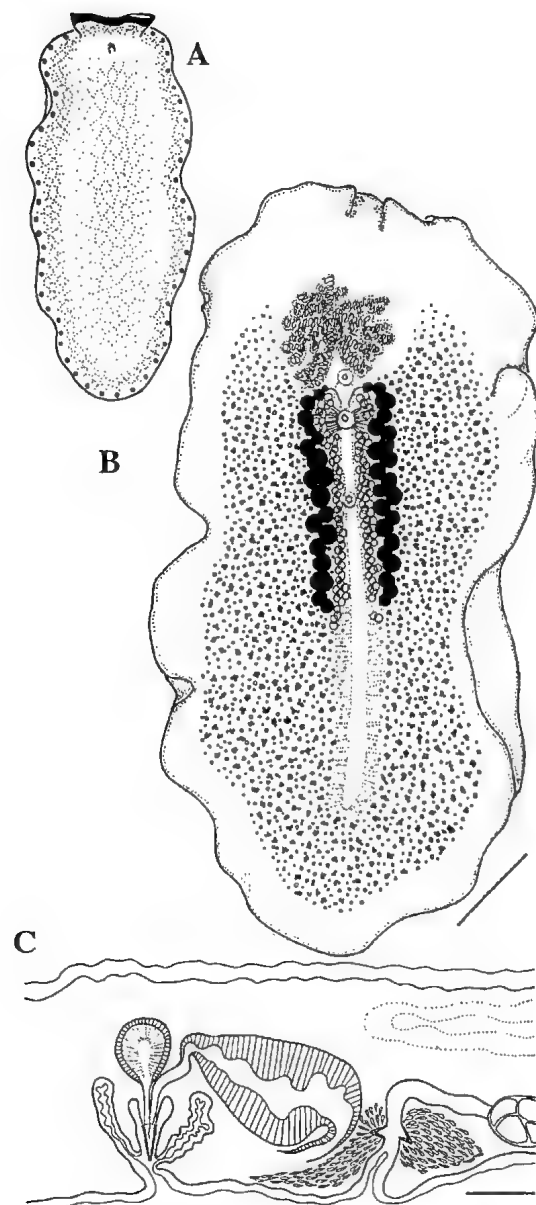


FIG. 24. *Pseudoceros ouini* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210631, wholemount showing the morphology from the ventral surface; C, QMG210631, reconstruction of the reproductive anatomy. Scales: 2mm; C, 250 μ m.

***Pseudoceros paralaticlavus* sp. nov.**
(Figs 25A - C; 48F)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 07.02.93, WM, QMG210432.

PARATYPES: Heron Is., reef crest, 07.09.92, WM, QMG210428; reef slope, 3m, 01.02.93, LS, QMG210431.

OTHER MATERIAL: Heron Is., reef crest, 17.10.89, WM, QMG210418; LS, QMG210459; 21.01.92, S, QMG210419; WM, QMG210420; 19.02.92, S, QMG210422; 07.08.92, WM, QMG210426; 03.09.92, WM, QMG210427; 17.02.93, S, QMG210435; One Tree Is., reef crest, 12.09.92, WM, QMG210429. Madang, reef crest, 3-5m, 01.06.92, LS, QMG210423; 08.06.92, LS, T. Gosliner, QMG210424; 11.06.92, WM, QMG210425; Planet Rock, S. Madang, reef slope, 6m, 26.05.92, S, QMG210436; Hansa Bay, Laing Is., reef crest, J. - M. Ouin, 15.06.92, WM, QMG210430.

DESCRIPTION

Colour & pattern. Background velvety black with wide cream-white median band and a narrow white median stripe. Two marginal bands; inner band wide, white; rim narrow, bright yellow (Process Yellow) or orange-yellow (109); pseudotentacles black with yellow rim. Ventrally same pattern. Pharynx sometimes dark purple (2695); ovaries and oviducts bright red-purple (226).

External features. Pseudotentacles simple folds. Cerebral eyespot with about 30 eyes. Size: mature from 22 \times 10mm to 50 \times 22mm; juvenile 9 \times 6mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle oblong (593 μ m long); ejaculatory duct long, coiled. Prostate round, extremely small (113 μ m wide). Stylet (165 μ m long) larger than prostate. Male and female antra shallow and wide.

DIAGNOSIS

Black with broad white longitudinal median stripe, margin with two bands: inner wide, white; outer narrow, yellow-orange.

ETYMOLOGY

From the Latin *para* = like, *laticlavus* = broad stripe, for its similarity in colour pattern to *P. laticlavus*.

REMARKS

This species belongs in Group 3 and is similar to *P. laticlavus*. However, *P. paralaticlavus* possesses a distinct yellow or orange marginal band and this band is absent in *P. laticlavus*. As well, *P. paralaticlavus* reaches a larger size at maturity (22 \times 10mm to 50 \times 22mm) compared to *P. laticlavus* (14 \times 8mm to 30 \times 10mm).

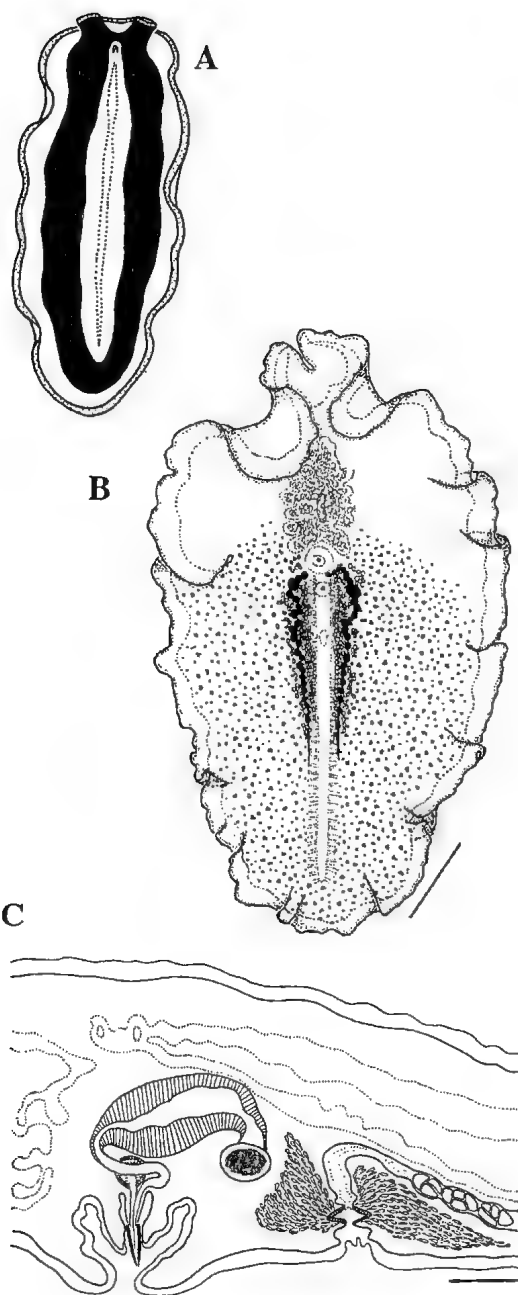


FIG. 25. *Pseudoceros paralaticlavus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210432, wholemount showing the morphology from the ventral surface; C, QMG210431, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 250 μ m.

HABITAT & DISTRIBUTION

Found on yellow colonial ascidians under boulders at the reef crest. Common from Heron Is., rare from Madang.

Pseudoceros periauranti sp. nov. (Figs 26A - C; 49A)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef slope, 6m, 30.07.92, WM, QMG210475.

PARATYPE: Heron Is., reef slope, 3m, 05.02.93, LS, QMG210476.

DESCRIPTION

Colour & pattern. Background velvety black with a distinct wide brilliant orange (136) marginal band. Ventrally dark grey with a lighter grey marginal band.

External features. Pseudotentacles broad flaps. Relatively small cerebral eyespot with about 50 eyes. Size: mature at 18 \times 12mm; juvenile at 30 \times 16mm.

Reproductive anatomy. Vas deferens not observed. Seminal vesicle small, round (413 μ m long); ejaculatory duct long, coiled. Prostate large, rounded oval (262mm wide). Stylet narrow (225 μ m long), similar in size to prostate. Male and female antra shallow.

REMARKS

This species belongs in Group 2. Several other species possess a black background and vibrantly coloured marginal bands. Only one other species has an orange marginal band, *P. litoralis*, but *P. periauranti* is black with an orange marginal band not brown with an orange inner marginal band and brown rim.

DIAGNOSIS

Black background with brilliant, wide orange marginal band.

ETYMOLOGY

From the Latin *peri* = around, *aurantius* = orange, for its distinct orange marginal band.

HABITAT & DISTRIBUTION

Found under ledges on the reef slope. Rare from Heron Is.

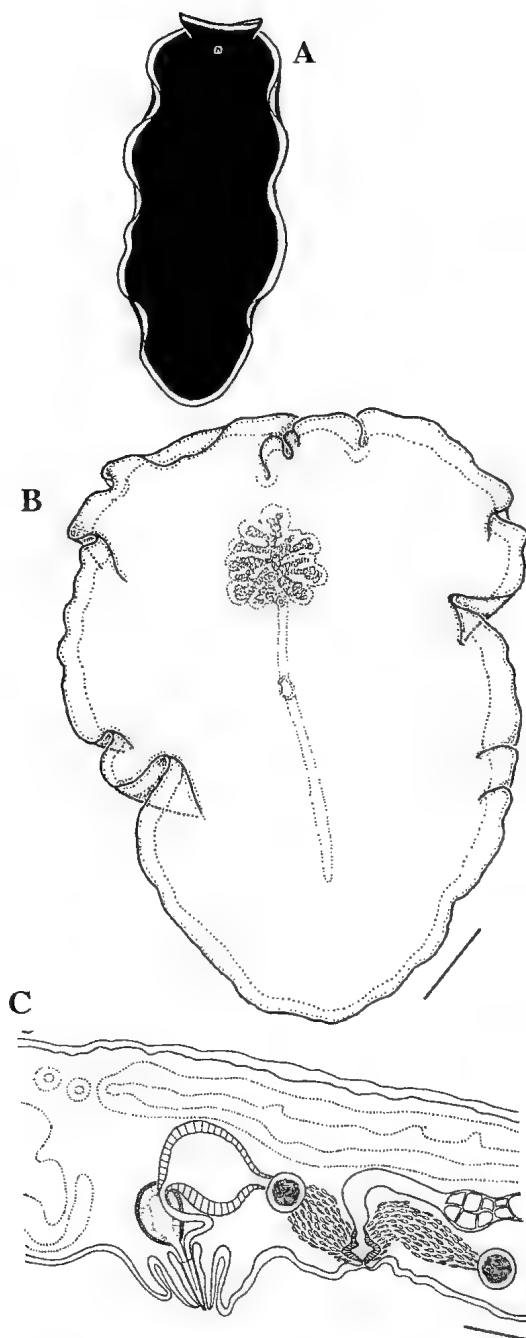


FIG. 26. *Pseudoceros periaurantiuss* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210475, wholemount showing the morphology from the ventral surface; C, QMG210476, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 250 μ m.

***Pseudoceros peripurpureus* sp. nov.**
(Figs 27A - C; 49B)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef slope, 21m, WM, 06.02.92, QMG210457.

PARATYPES: Heron Is., reef slope, 21m, LS, QMG210456; 10m, night, 25.02.92, LS, QMG210458.

DESCRIPTION

Colour & pattern. Background velvety black with two distinct narrow marginal bands; inner band violet (245), dark purple (2735) at rim. Ventrally dark blue-black, same marginal bands.

External features. Large species, body thick and fleshy, tapering slightly posteriorly. Pseudotentacles broad flaps. Eyes obscured by black pigment. Size: mature from 40 \times 25mm to 60 \times 35mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle large, oblong (1.8mm long); ejaculatory duct coiled. Prostate oval (398 μ m wide). Stylet long (223 μ m long). Male and female antra shallow.

DIAGNOSIS

Black with two narrow marginal bands; inner violet, outer purple.

ETYMOLOGY

From the Latin *peri* = around, *purpureus* = purple, for its purple marginal bands.

REMARKS

This species belongs in Group 2 in which several species possess a black background with vibrantly coloured marginal bands, however, no other species has a purple marginal band. Hyman (1959a) described *Pseudoceros caeruleocinctus* as having a brilliant blue marginal band but it is uncertain whether this species belongs to *Pseudoceros* since morphological details were not given. Although the holotype was examined, the shape of the pharynx could not be ascertained due to the black pigmentation and the contracted nature of the specimen.

HABITAT & DISTRIBUTION

Found under ledges on the reef slope. Rare from Heron Is.

***Pseudoceros prudhoei* sp. nov.**
(Figs 28A - C; 49C)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 14.09.89, WM, QMG210398.

PARATYPES: 23.08.92, LS, QMG210402; 23.02.93, LS, QMG210403.

OTHER MATERIAL: Heron Is., reef crest, 05.02.92, WM, QMG210399; Madang, reef crest, 2 - 5m, T. QMGosliner, 06.06.92, S, QMG210442; 09.06.92, WM, QMG210400; WM, QMG210401; 01.06.92, S, 2 spec., QMG210434; 24.06.92, S, 2 spec., 24.06.92, QMG210433.

DESCRIPTION

Colour & pattern. Background brown-orange (143) with two marginal bands: inner band wide, sky blue (290 or 306) or mauve (5315); outer band distinct, narrow, yellow (102 or 393) or cream. Entire dorsal surface covered in dark brown microdots. Ventrally same colour pattern.

External features. Margin with few ruffles. Pseudotentacles simple folds. Cerebral eyespot relatively small with 30 to 50 eyes. Size: mature from 30 × 8mm; juvenile from 7 × 3mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle elongate oblong (638µm long); ejaculatory duct short, not coiled. Prostate round (248µm wide). Stylet long (225µm long), similar size to prostate. Male antrum deep, voluminous. Female antrum deep.

DIAGNOSIS

Brown covered in brown microdots: two marginal bands; inner band wide, blue or light purple; outer band narrow, bright yellow.

ETYMOLOGY

In honour of the late Mr Stephen Prudhoe.

REMARKS

This species belongs in Group 2. Only *P. litoralis* also possesses a brown background colour with two marginal bands, however, in *P. prudhoei* the marginal bands are blue and yellow not orange and black.

HABITAT & DISTRIBUTION

Found under boulders and under rubble at reef crest. Rare from Heron Is. and Madang.

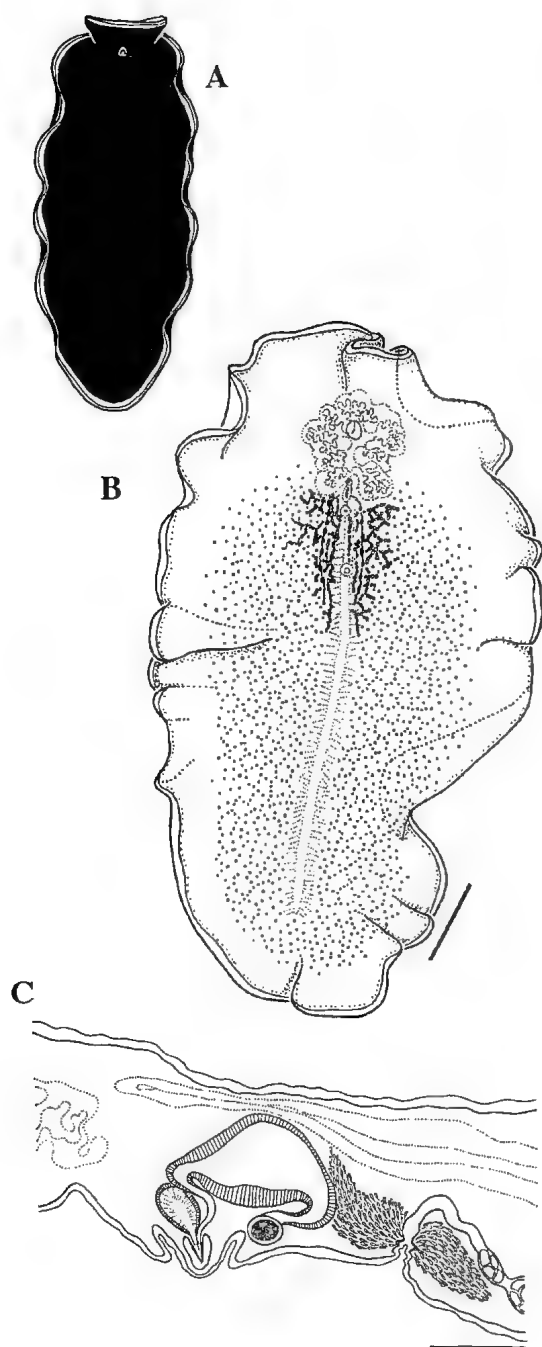


FIG. 27. *Pseudoceros peripurpureus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210457, wholemount showing the morphology from the ventral surface; C, QMG210458, reconstruction of the reproductive anatomy. Scales: B, 5mm; C, 500µm.

***Pseudoceros sapphirinus* sp. nov.**
(Figs 29A - C; 49D)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef slope, 10m, night, 29.01.92, WM, QMG210444.

PARATYPES: Heron Is., reef slope, 12m, 25.02.92, LS, QMG210445; 10m, 04.09.92, LS, QMG210447.

OTHER MATERIAL: Heron Is., reef slope, 6 - 10m, 26.06.91, LS, QMG210443; 20.01.92, WM, QMG210488; night, 25.02.92, S, QMG210446; One Tree Is., reef slope, 15m, 17.08.93, QMG210522. Other Record: Philippines, 10 km S of Anilao, reef slope, 10m, night, T. Gosliner, 26.06.93, CT.

DESCRIPTION

Colour & pattern. Background velvety black with a wide bright royal blue lateral band (near but not at the margin); extremely narrow bright white (sometimes yellow or turquoise) line at rim. Ventral surface velvety black with white rim.

External Features. Margin not ruffled, body thick and fleshy. Pseudotentacles broad flaps. Cerebral eyespot with about 40 eyes. Pseudotentacular eyes not visible due to dark pigment. Size: mature 35 × 20mm to 58 × 30mm; juvenile from 16 × 8mm.

Reproductive anatomy. Seminal vesicle large (1.0mm long); ejaculatory duct long, coiled. Prostate round (315µm wide). Stylet small (130µm long). Male and female antra deep.

DIAGNOSIS

Black with vibrant blue lateral band and extremely narrow white rim.

ETYMOLOGY

From the Latin *sapphirinus* = sapphire, for its brilliant sapphire- blue lateral band.

REMARKS

This species belongs in Group 2 in which several species possess a black background and vibrantly coloured marginal bands but only in *P. sapphirinus* is the band located laterally, not at the margin. This species is similar in colour to *P. peripurpureus* which possesses marginal bands of purple and violet rather than a lateral blue band. *P. caeruleocinctus* Hyman, 1959a was also described as black with a blue margin (not a lateral band as in *P. sapphirinus*), however, the validity of the species remains uncertain.

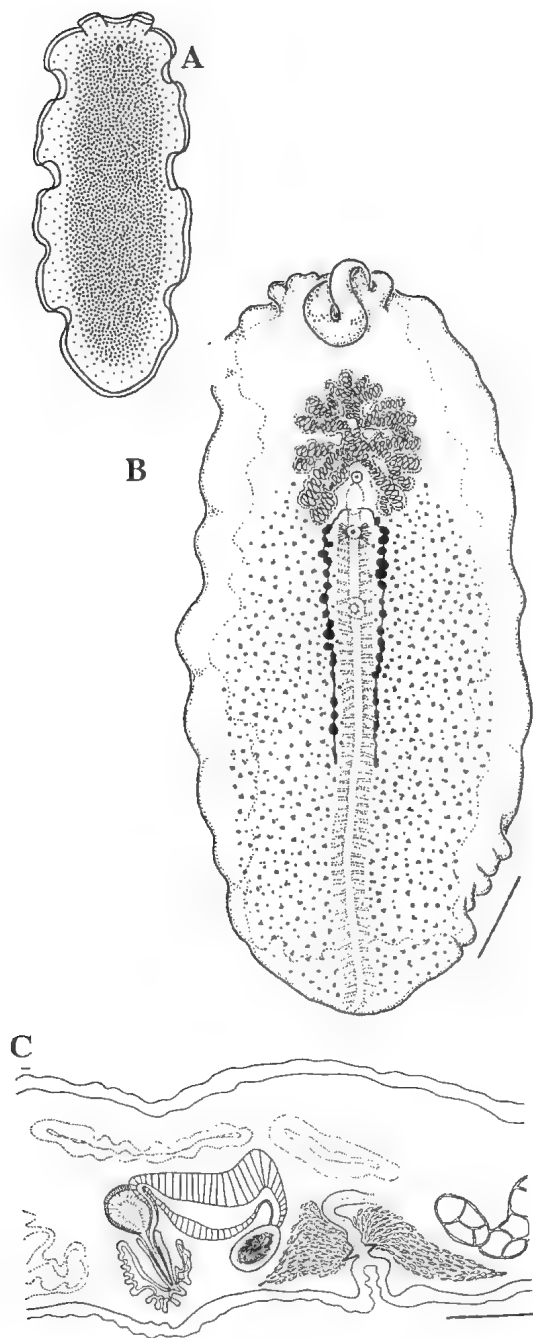


FIG. 28. *Pseudoceros prudhoei* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210398, wholemount showing the morphology from the ventral surface; C, QMG210402, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 500µm.

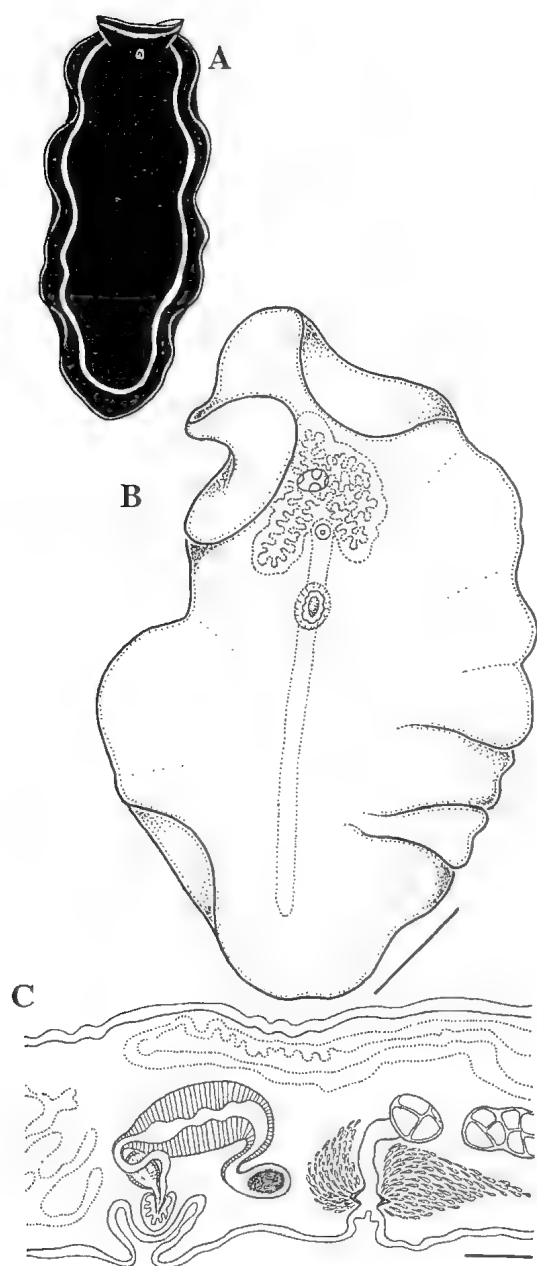


FIG. 29. *Pseudoceros sapphirinus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210444, wholemound showing the morphology from the ventral surface; C, QMG210447, reconstruction of the reproductive anatomy. Scales: B, 2mm; C, 500 μ m.

BIOLOGY

Often observed moving across live coral (*Acropora* sp.) during the day and night. This species extrudes a dark red mucus when disturbed.

HABITAT & DISTRIBUTION

Found under ledges on the reef slope, especially at night. Common from Heron Is. Record: Philippines.

Pseudoceros scintillatus sp. nov. (Figs 30A - C; 49E)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 15.08.92, WM, QMG210629.

PARATYPE: Heron Is., reef crest, 01.08.92, LS, QMG210628.

DESCRIPTION

Colour & pattern. Background velvety black with a bold pattern of large irregularly sized yellow-green maculae (393); maculae extend into the marginal band, each macula encircled by white. Marginal band distinct, wide orange (137).

External features. Small species. Pseudotentacles simple folds. Size: mature 9 \times 4mm; juvenile 6 \times 2mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle small, rounded oval (413 μ m long). Prostate rounded small, oval (143 μ m wide). Stylet relatively short (135 μ m long), slightly longer than the prostate. Male and female antra shallow.

DIAGNOSIS

Black with large irregular yellow-green maculae and orange marginal band.

ETYMOLOGY

From the Latin *scintillatus* = scintillating, for its dramatic colour pattern.

REMARKS

This species belongs in Group 5. Two other species are similar, *P. lindae* and *P. glaucus*. However, *P. scintillatus* is black with yellow-green maculae not burgundy with golden-yellow and blue maculae as in *P. lindae* or grey with black maculae as in *P. glaucus*. *P. scintillatus* also resembles *P. mossambicus* (Group 4) which possesses spots (not maculae).

HABITAT & DISTRIBUTION

Found on colonial ascidians under boulders at reef crest. Rare from Heron Is.

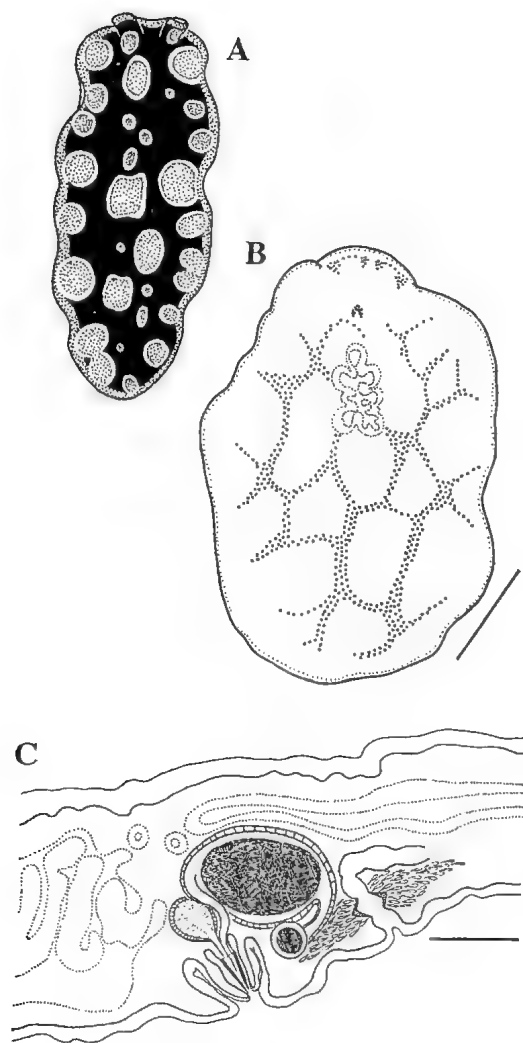


FIG. 30. *Pseudoceros scintillatus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210629, wholemount showing the morphology from the ventral surface; C, QMG210628, reconstruction of the reproductive anatomy. Scales: B, 1mm; C, 250 μ m.

***Pseudoceros verecundus* sp. nov.**
(Figs 31A - C; 49F)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 08.09.92, WM, QMG210409.

PARATYPE: Heron Is., reef crest, 18.02.93, LS, QMG210410.

OTHER MATERIAL: Heron Is., reef crest, 15.09.89, S, QMG210404; 24.06.91, S, QMG210437; 30.07.92, WM, QMG210405; 01.08.92, WM, QMG210406;

02.08.92, WM, QMG210407; 15.08.92, WM, QMG210408; One Tree Is., 19.08.93, WM, QMG210499.

DESCRIPTION

Colour & pattern. Background cream-white with orange microdots over the entire surface. Two discontinuous or interrupted narrow lateral bands (near but not at the margin): inner band narrow, black; outer wide, orange-brown (144). Margin cream-white with a narrow lemon yellow rim. Three distinct marginal bands across the pseudotentacles; inner band orange-brown, middle band black, yellow (102) at rim. Faint black triangle with one large median white spot anteriorly between pseudotentacles. Few animals found with light brown microdots forming faint blotches medially. Ventrally cream.

External features. Pseudotentacles simple folds. Cerebral eyespot with about 40 eyes. Size: mature from 20 \times 8mm to 26 \times 14mm; juvenile from 10 \times 5mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle rounded oblong (645 μ m long), ejaculatory duct short, coiled. Prostate rounded oval (188 μ m wide). Stylet small (113 μ m long). Male and female antra deep.

DIAGNOSIS

Cream with interrupted orange and black lateral bands: pseudotentacles with three marginal bands; orange, black and yellow.

ETYMOLOGY

From the Latin *verecundus* = demure, for its cryptic colour pattern.

REMARKS

This species belongs in Group 2. Three other species possess a cream background, however, no other species has interrupted lateral bands. This species most resembles *P. bimarginatus* which has three marginal band around the entire margin, however, in *P. verecundus* the marginal bands cover only the pseudotentacles. This species is also similar to *P. heronensis* (Group 4) but *P. verecundus* is covered with microdots (not spots and blotches medially) and the tricoloured marginal bands cover only the pseudotentacles (not the pseudotentacles and posterior end).

HABITAT & DISTRIBUTION

Found feeding on cream-white colonial ascidians. Common from Heron Is. Rare from One Tree Is.

Pseudobiceros Faubel, 1984

Pseudobiceros strigosus (Marcus, 1950)[junior synonym of *P. gratus* (Kato, 1937)]: Unknown, painting only?

TYPE LOCALITY
Ceylon.

EMENDED DIAGNOSIS

Flamboyantly or cryptically coloured. Body soft and extremely delicate, raised medially, elongate oval, tapering posteriorly, margin with numerous deep ruffles (Fig. 2B). Pseudotentacles well developed, either pointed and ear-like or square with lateral ruffles (Fig. 3C, D). Cerebral eyespot small, horseshoe shaped, with 20 to 200 eyes in semi-circular rows, eyespot in a clear area which is pointed anteriorly and posteriorly. Dorsal pseudotentacular eyes in four elongate clusters (not along the anterior margin), ventral pseudotentacular eyes in four dense clusters extending medially over the pseudotentacles, with 100's of eyes (Fig. 3F). Pharynx anterior, oval, with 10 to 20 shallow simple pharyngeal folds (Figs. 4B, 5B). Intestine wide, extends to about 2/3 body length, numerous extremely narrow intestinal branches not extending to the posterior end of the intestine. Two symmetrical male pores are posterior to pharynx, male apparatus double, and identical. Female pore between and usually close to male pores. Sucker indistinct, three to five times the distance between the gonopores. Male copulatory apparatus double, each with seminal vesicle and armed penis papilla. Prostatic vesicle orientated to the male complex antero-dorsally.

TAXONOMIC REMARKS

Faubel (1984) erected *Pseudobiceros* on the basis of the double male apparatus and described the genus as: 'Pseudocerotidae with smooth dorsal surface and elongate oval outline. Tentacular and cerebral eyespots present. Male copulatory apparatus double, each with seminal vesicle and armed penis papilla. Prostatic vesicle orientated to the male complex antero-dorsally.' Although Faubel's name appears etymologically incorrect (these worms do not have paired pseudotentacles, but paired male systems), it is quite valid.

LIST OF RECOGNISED SPECIES

The following 14 known species we believe may be reliably placed in *Pseudobiceros* sensu

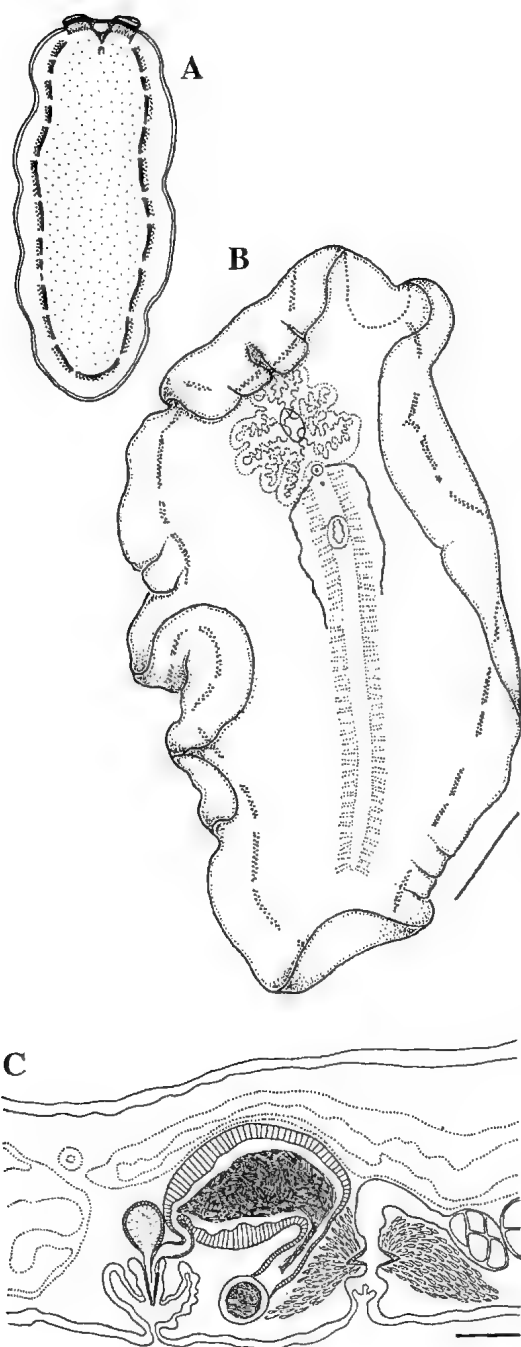


FIG. 31. *Pseudoceros verecundus* sp. nov.: A, diagram of the dorsal colour pattern; B, QMG210409, wholemount showing the morphology from the ventral surface; C, QMG210410, reconstruction of the reproductive anatomy. Scales: B, 2mm; C, 250µm.

TABLE 2. Colour pattern groups for recognised and new species of *Pseudobiceros*

| # | Colour Pattern | Recognised Species | New Species |
|---|------------------------------|--|--|
| 1 | Even Colour | none | none |
| 2 | Marginal Bands | <i>evelinae</i> - red; orange & black margin <i>hancockanus</i> * - black; orange & white margin <i>splendidus</i> - black; orange & brown margin | <i>flavocanthus</i> - black; white & yellow margin <i>gloriosus</i> - black; orange & pink & purple margin <i>periculosus</i> - black; orange margin <i>uniarboretus</i> - black; orange, grey & white margin |
| 3 | Longitudinal Stripes | <i>cincereus</i> - black; 2 grey stripes, grey margin <i>gratus</i> * - white; 3 or 4 black stripes <i>nigromarginatus</i> - black; 2 brown stripes, black margin <i>philippinensis</i> - black; 3 purple-grey stripes, orange margin | none |
| 4 | Spots, Dots & Mottling | <i>bajae</i> - black; sometimes white irregular dots <i>fulvogriseus</i> - grey; mottled yellow & brown <i>gardineri</i> - grey; mottled black <i>izuensis</i> - white; black dots; interrupted margin | <i>apricus</i> - orange; white dots, black margin <i>damawan</i> - grey & white; black spots, orange margin <i>stellae</i> - black; white regular dots |
| 5 | Maculae | none | none |
| 6 | Transverse Streaks & Stripes | <i>bedfordi</i> * - black; yellow dots, pink streaks <i>dendriticus</i> - yellow; mottled brown, yellow stripes <i>flavolineatus</i> - brown; yellow stripes, black margin | <i>fulgor</i> - brown; yellow & white stipes, black margin |

* collected during this study

stricto based on the morphology of the pharynx, eyes, pseudotentacles or reproductive anatomy (Table 2): *bajae* (Hyman, 1953) comb. nov.; *bedfordi* (Laidlaw, 1903)*; *cincereus* (Palombi, 1931); *dendriticus* (Prudhoe, 1989); *evelinae* (Marcus, 1950); *flavolineatus* (Prudhoe, 1989); *fulvogriseus* (Hyman, 1959); *gardineri* (Laidlaw, 1902); *gratus* (Kato, 1937)*; *hancockanus* (Collingwood, 1876) comb. nov.*; *izuensis* (Kato, 1944); *nigromarginatus* (Yeri & Kaburaki, 1918); *philippinensis* (Kaburaki, 1923); *splendidus* (Lang, 1884)(*collected during this study).

Species from eastern Australia & Papua New Guinea

***Pseudobiceros apricus* sp. nov.**
(Figs 32A - D; 50A)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 02.02.92, WM, QMG210585.

PARATYPE: Heron Is., reef crest, 22.02.93, LS, QMG210577.

OTHER MATERIAL: Heron Island, reef crest, 28.12.90, WM, QMG210571; 30.12.90, WM, QMG210572; 02.01.91, WM, QMG210573; 18.01.92, WM, QMG210580; 23.01.92, WM, QMG210582; S, QMG210583; 31.01.92, S, QMG210584; 02.02.92,

WM, QMG210586; 14.02.92, WM, QMG210587; 16.02.92, LS, QMG210588; 19.02.92, LS, QMG210589; S, QMG210590; 18.02.93, S, QMG210574; 20.02.93, S, QMG210576; 21.02.93, S, QMG210575; 22.02.93, LS, QMG210578; One Tree Is., reef crest, 16.08.93, WM, QMG210579.

DESCRIPTION

Colour & pattern. Background transparent orange (178); entire dorsal surface covered with raised white microdots and irregular scattered clusters of larger white dots, darker pigment medially. Marginal band narrow, black with white dots. Pseudotentacles grey-black with white tips. Gut diverticula sometimes bright orange.

External features. Pseudotentacles square with slight lateral ruffles. Cerebral eyespot with about 30 eyes in a clear round area. Two male pores close together. Size: mature from 24 × 10mm to 60 × 25mm; juvenile from 5 × 2mm.

Reproductive anatomy. Unbranched vas deferens. In one system: seminal vesicle oval (713µm long), ejaculatory duct short, coiled; prostate round (263µm wide); stylet long (368µm long). Male and female antra shallow.

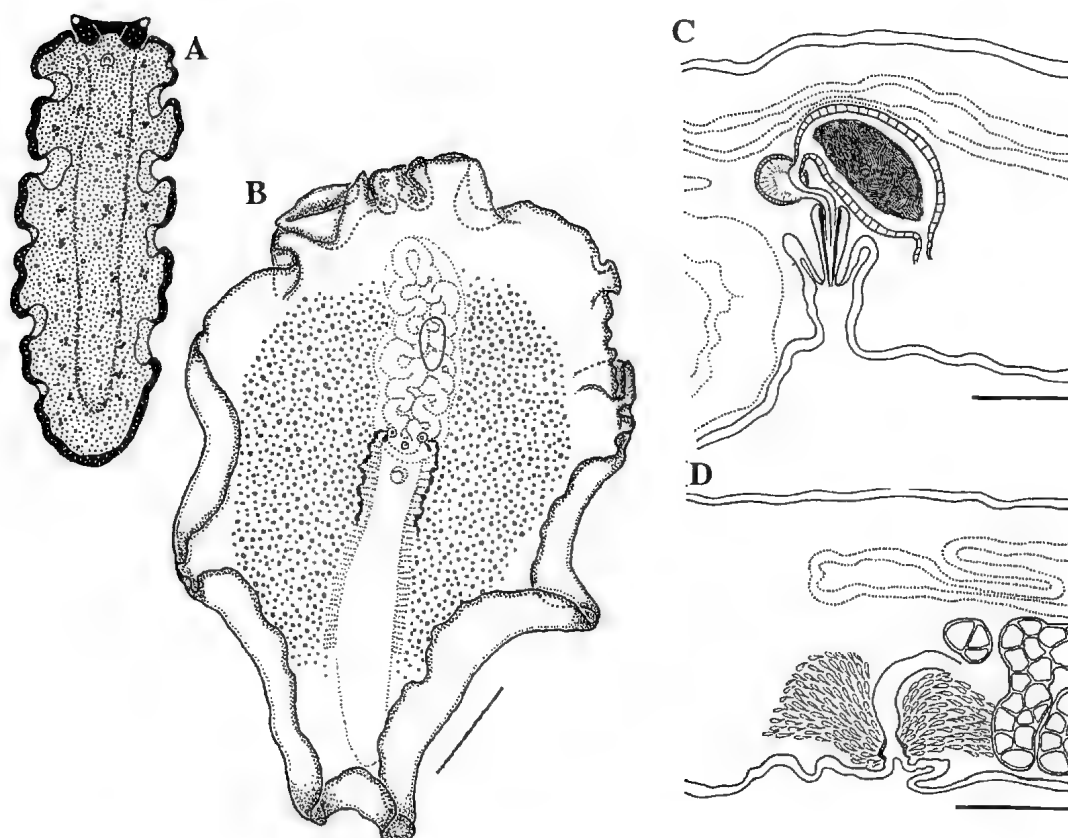


FIG. 32. *Pseudobiceros apricus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210585 wholemount showing the morphology from the ventral surface; C, D, QMG210577, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 2mm; C, D, 500 μ m.

DIAGNOSIS

Transparent orange with raised white microdots, black marginal band with white dots.

ETYMOLOGY

From the Latin *apricus* = orange, for its apricot-like colour.

REMARKS

This species belongs in Group 4 where the majority of species are black or grey. No other species possesses an orange background and white microdots (Table 2).

HABITAT & DISTRIBUTION

Found on pink colonial ascidians under boulders at the reef crest. Common from Heron Is., rare from One Tree Is.

Pseudobiceros bedfordi (Laidlaw, 1903) (Figs 33A - D; 50B)

Pseudoceros bedfordi Laidlaw, 1903: 302, 314, pl. 23, fig. 9; Bock, 1913: 254, pl. III, figs 2 - 4; Bresslau, 1933: 59; Kato, 1943, 87; 1944: 299; Marcus, 1950: 84; Dawydoff, 1952: 82; Hyman, 1954: 220; 1959: 566; Prudhoe, 1977: 586; George & George, 1979: 43, pl. 49, fig. 10.

Pseudoceros micronesianus Hyman, 1955: 66, fig. 5.
Pseudobiceros bedfordi (Laidlaw, 1903): Faubel, 1984: 216.

MATERIAL EXAMINED

HOLOTYPE: Unknown, painting only?, Singapore.
OTHER MATERIAL: Heron Is., reef slope, 7 - 10m, 28.04.89, S, QMG210513; 16.06.91, WM, QMG210509; 19.06.91, LS, QMG210510; 26.06.91, S, QMG210511; 22.01.92, LS, QMG210512; 27.01.92, S, QMG210514; 31.01.92, WM,

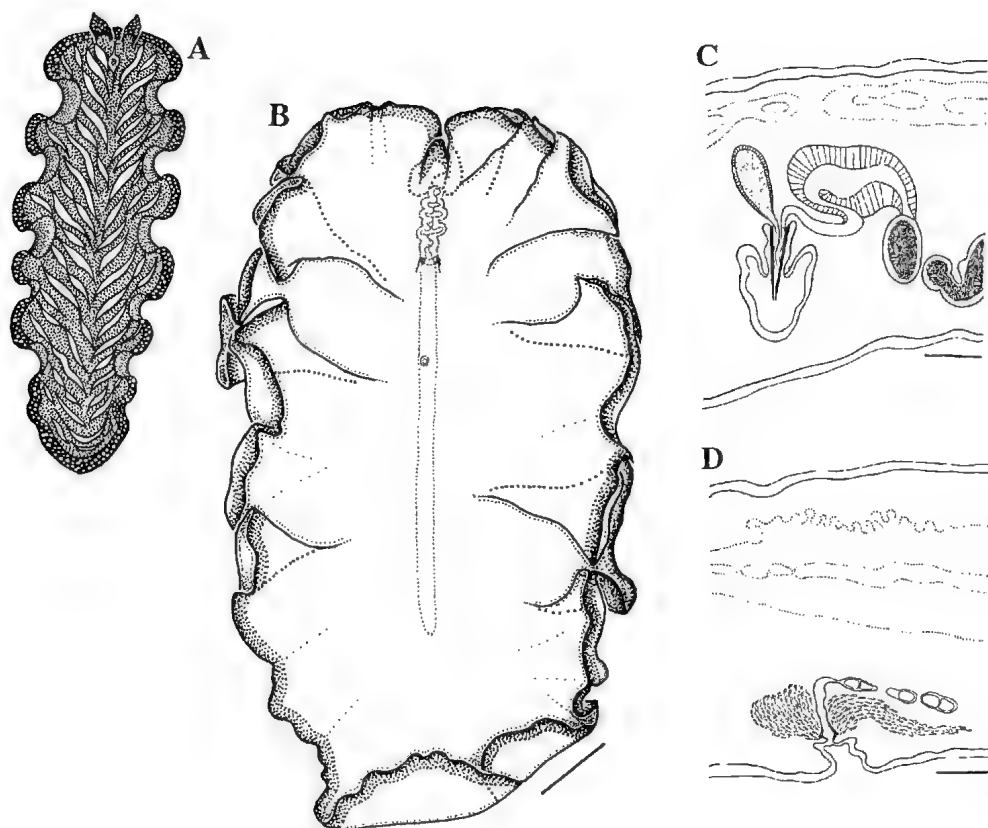


FIG. 33. *Pseudobiceros bedfordi* (Laidlaw, 1903). A, diagram of the dorsal colour pattern; B, QMG210509 wholemount showing the morphology from the ventral surface; C, D, QMG210519 reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 2.5mm; C, D, 250 μ m.

QMG210515; 05.02.92, WM, QMG2105, WM; 08.08.92, LS, QMG210518; J. Tanner, 03.09.92, LS, QMG210519; 05.02.93, S, QMG210521; Madang, reef slope, 4m on rubble, night, 03.06.92, LS, QMG210517; Hansa Bay, Laing Is., reef flat, 1m, J.-M. Ouin, 09.06.92, WM, QMG210520.

DESCRIPTION

Colour & pattern. Background colour varies from brown to black with numerous compacted bright yellow dots; numerous transverse bilateral streaks of pink (190) outlined in black, variable in shape; yellow dots more concentrated between the streaks. Margin black with white dots. Ventrally deep pink (191) with black marginal band.

External features. Pseudotentacles pointed and ear-like. Cerebral eyespot with about 100 eyes. Pharynx small. Male pores close together. Sucker well separated from gonopores. Size: mature from 29 \times 18mm to 100 \times 45mm; juvenile from 25 \times 12mm.

Reproductive anatomy. Vas deferens unbranching. In one system: seminal vesicle short (1.0mm long), ejaculatory duct long, coiled; prosotate large, oval (796 μ m wide); stylet extremely long, narrow (592 μ m long). Male and female antra shallow.

REMARKS

This species belongs in Group 6 and is similar to *P. dendrictus* and *P. flavolineatus*. *P. bedfordi* is black, yellow and pink not yellow and brown

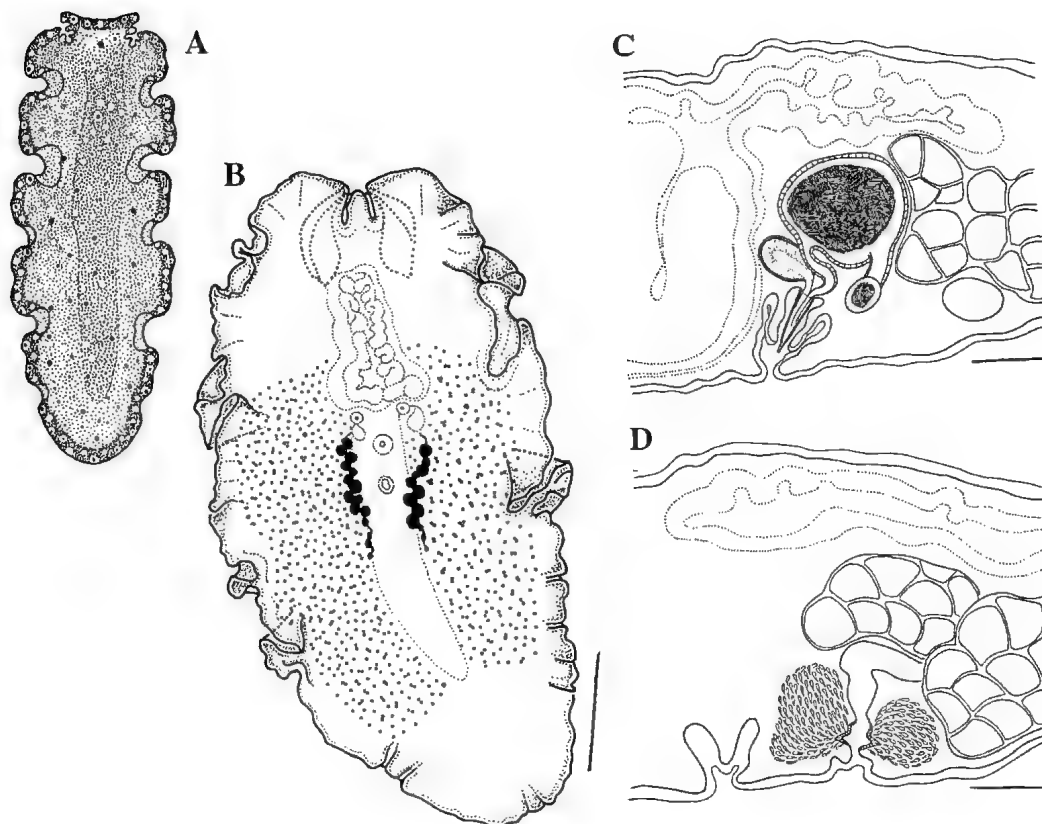


FIG. 34. *Pseudobiceros damawan* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210613, wholemount showing the morphology from the ventral surface; C, D, QMG210607, reconstruction of the reproductive anatomy. C, one male system; D, the female system. Scales: B, 2.5mm; C, D, 250µm.

as in *P. dendrictus* and has wide streaks not narrow lines as in *P. flavolineatus*.

Pseudoceros micronesianus Hyman, 1955 (Holotype, USNM25947 was examined) is considered a synonym of this species since the pattern as described by Hyman (based on a damaged preserved specimen) clearly resembles the pattern after fixation in *P. bedfordi*.

BIOLOGY

Eggmasses were laid on the side of an ice cream container. Müller's larvae hatched within 10 days.

HABITAT & DISTRIBUTION

Found under boulders at the reef crest and under ledges on the reef slope. Common from Heron Is.; rare from Madang and Laing Is.

Records: GBR, Singapore, Philippines, Micronesia.

Pseudobiceros damawan sp. nov. (Figs 34A - D; 50C)

MATERIAL EXAMINED

HOLOTYPE: Laing Is., reef crest, J.-M. Ouin, 15.09.92, LS, QMG210613.

PARATYPE: Laing Is., reef crest, J.-M. Ouin, 15.09.92, WM, QMG210612.

OTHER MATERIAL: Madang, reef crest, 3 - 5m, 27.05.92, WM, QMG210603; WM, QMG210604; S, QMG210605; 11.06.92, WM, QMG210606; S, QMG210608; S, QMG210609; The Quarry, 40 km N Madang, reef slope, 10m, 13.06.92, WM, QMG210610; Heron Is., reef slope, 10m, 09.09.92, LS, QMG210611.

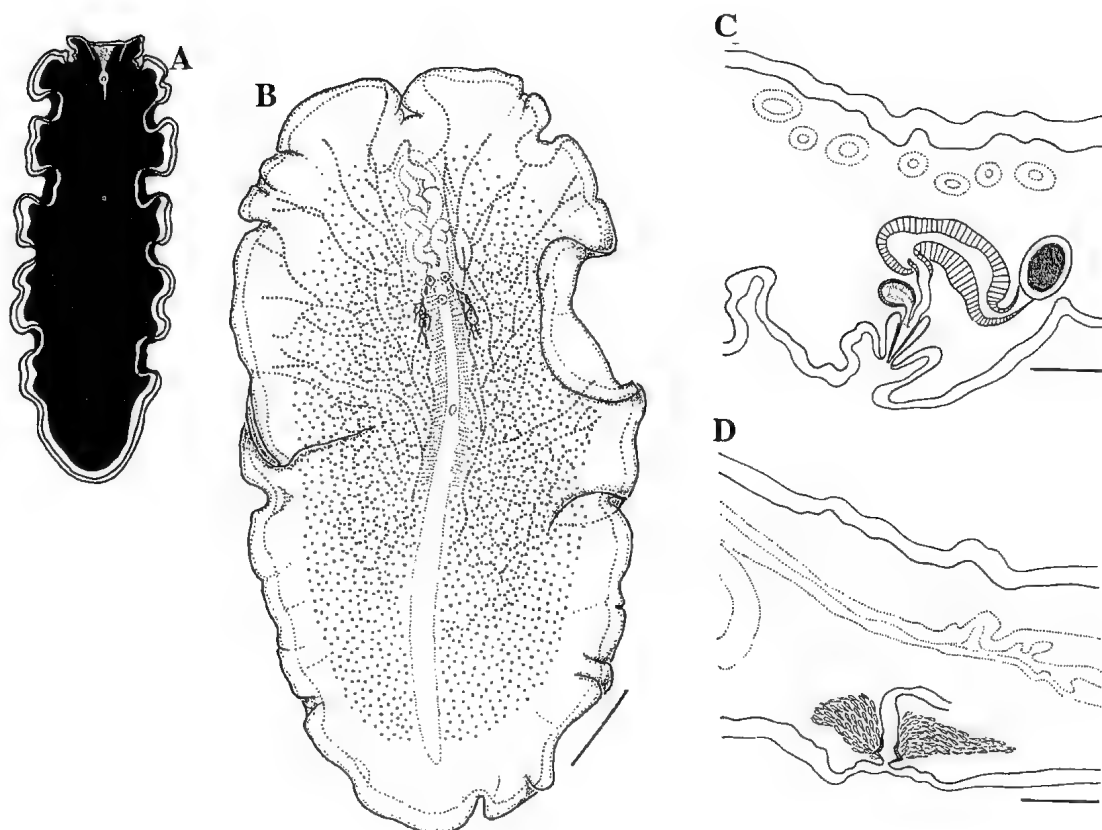


FIG. 35. *Pseudobiceros flavocanthus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210470, wholemount showing the morphology from the ventral surface; C,D, QMG210471, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 5mm; C, D, 500µm.

DESCRIPTION

Colour & pattern. Background mottled, transparent grey and opaque white with widely spaced black spots over the entire surface. Light orange (163) medially, marginal band orange (163) interrupted with white spots; extremely narrow black rim. Ventral surface cream with a mottled orange marginal band and black rim.

External features. Pseudotentacles square and ruffled. Cerebral eyespot small, round with about 50 eyes. Male pores well separated. Size: mature from 10 × 5mm to 18 × 8mm; juvenile from 1.5 × 0.5mm.

Reproductive anatomy. Vas deferens unbranched. In one system: seminal vesicle round,

short (413µm long); ejaculatory duct short, coiled; prostate small, oval (203µm wide); stylet small (135µm long), larger than the prostate. Male and female antra shallow.

DIAGNOSIS

Mottled grey and white, orange medially and laterally, covered in sparse black spots.

ETYMOLOGY

From the Rewo Village language (Madang, PNG) name of the reef where it was collected.

REMARKS

This species belongs in Group 4. Two other species are mottled grey, *P. fulvogriseus* and *P. gardineri*, however, only *P. damawan* possesses an orange margin and black spots. Cryptic especially when found on colonial ascidians.

HABITAT & DISTRIBUTION

Found on colonial ascidians under boulders at reef crest and on reef slope. Common from Madang. Rare from Laing and Heron Islands.

***Pseudobiceros flavocanthus* sp. nov.**
(Figs 35A - D; 50D)

MATERIAL EXAMINED

HOLOTYPE: Madang, reef crest, 3m, 29.06.92, WM, QMG210616.

PARATYPE: Madang, reef crest, 3m, 16.06.92, LS, QMG210615.

DESCRIPTION

Colour & pattern. Background velvety black with two narrow marginal bands of equal width; inner band white, outer band narrow, bright yellow. White-grey triangle between the pseudotentacles extending into the cerebral eyespot. Ventrally grey with same marginal bands.

External features. Pseudotentacles small, square and slightly ruffled. Cerebral eyespot round with about 30 eyes. Male pores extremely close together. Sucker well separated from gonopores. Size: mature from 35 × 15mm to 50 × 16mm.

Reproductive anatomy. Vas deferens branched, testes forming network throughout the body. In one system: seminal vesicle elongate, small (465µm long); ejaculatory duct short, not coiled; prostate round, extremely small (135µm wide). Male and female antra shallow.

DIAGNOSIS

Black with two narrow marginal bands; inner white and outer yellow.

ETYMOLOGY

From the Latin *flavo* = yellow, *canthus* = ribbon, for its conspicuous yellow marginal band.

REMARKS

This species belongs in Group 2 in which the majority of species possess a black background, however, only *P. uniareborensis* sp. nov. and *P. hancockanus* have similar coloured marginal bands.

HABITAT & DISTRIBUTION

Found under rubble at reef crest. Rare from Madang.

***Pseudobiceros fulgor* sp. nov.**
(Figs 36A - D; 50E)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 24.02.93, S, QMG210559.

PARATYPES: Heron Is., reef crest, 10.08.92, LS, QMG210556; reef slope, 20m, 05.09.92, LS, QMG210557.

OTHER MATERIAL: 28.09.89, S, QMG210552; 19.01.92, S, QMG210553; 02.02.92, WM, QMG210554; 14.02.92, WM, QMG210555; 20.02.93, S, QMG210558. Records: 10 km S. Anilao, Philippines, 10m, night, T. Gosliner, 26.03.93, CT.

DESCRIPTION

Colour & pattern. Background orange-brown (143) or deep pink (184), intensifying toward the margin; numerous fine broken irregular longitudinal and transverse, short white stripes; yellow or cream blotches dispersed evenly over the entire surface. Margin black with numerous white streaks, parallel to the rim. Ventral surface light orange-brown (141) with a black marginal band.

External features. Extremely fragile species. Pseudotentacles pointed and ear-like. Cerebral eyespot relatively small, elongate with about 60 eyes. Pharynx relatively small. Size: mature from 38 × 20mm to 70 × 38mm; juvenile from 5 × 2mm.

Reproductive anatomy. Vas deferens unbranched. In one system: seminal vesicle rounded (740µm long); ejaculatory duct extremely short, not coiled; prostate oval (370µm wide); stylet short (158µm long). Male and female antra extremely shallow.

DIAGNOSIS

Light brown background and black margin with fine white broken stripes.

ETYMOLOGY

From the Latin *fulgor* = lightning, for its fine white and yellow broken stripes.

REMARKS

This species belongs in Group 6. Only *P. flavolineatus* also possesses a brown background, however, *P. fulgor* possesses broken streaks not concentric stripes as in *P. flavolineatus*. *P. fulgor* is similar to *Pseudoceros cerebralis* (Kelaart, 1858) which is described as

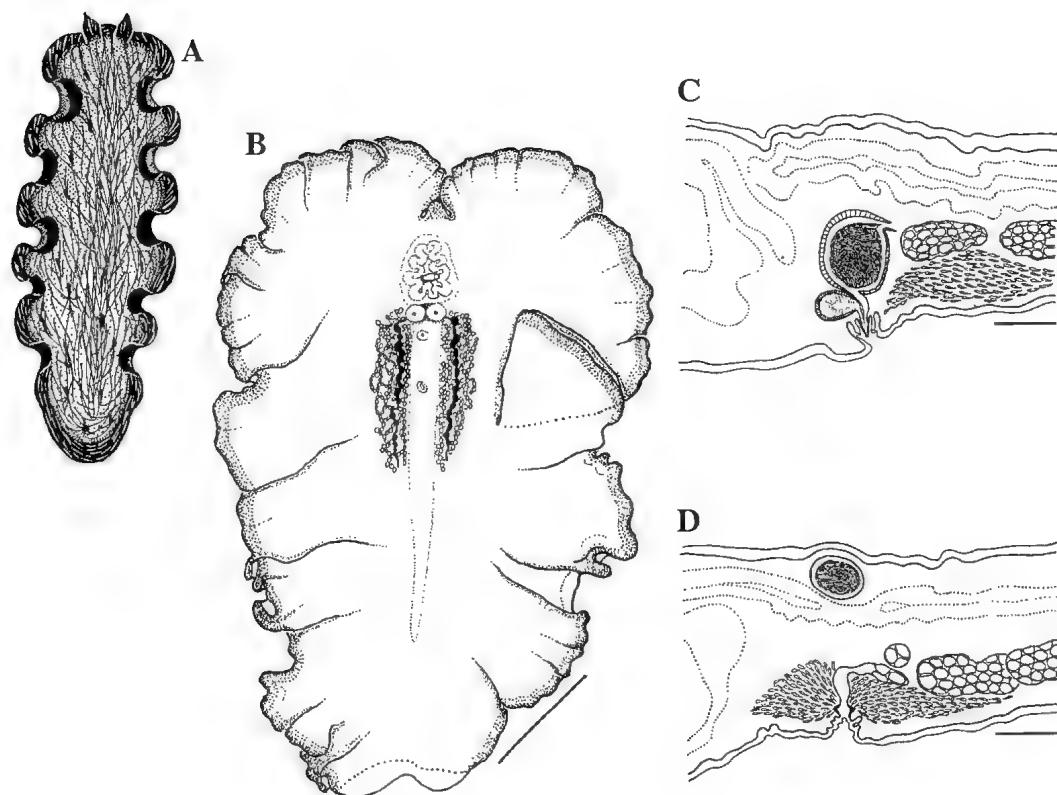


FIG. 36. *Pseudobiceros fulgor* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210559, wholemount showing the morphology from the ventral surface; C, D, QMG210556, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 5mm; C, D, 500µm

having broken brown stripes (not yellow or white), but the validity of *P. cerebralis* is uncertain as the number of male pores and morphology of the pharynx was not given.

BIOLOGY

This species extrudes copious amounts of transparent mucus and animals readily disintegrated during collection.

HABITAT & DISTRIBUTION

Found under boulders at reef crest. Common from Heron Is. Record: Philippines.

Pseudobiceros gloriosus sp. nov. (Figs 37A - D; 50F)

MATERIAL EXAMINED

HOLOTYPE: Bagabag Is., 62 km NE Madang, reef slope, 30.06.92, WM, QMG210549.

OTHER MATERIAL: Heron Is., reef slope, 6 -15m, M. McCarthy, 20.09.89, WM, QMG210546; 19.01.92, LS, QMG210547; 05.02.92, LS, QMG210548; 10.09.92, LS, QMG210550; 17.02.93, S, QMG210551. Record: Namalata Reef, Kadavu, Fiji, reef slope, 12m, J. Marshall, 07.07.93, CT.

DESCRIPTION

Colour & pattern. Background velvety black with three marginal bands: inner band wide,

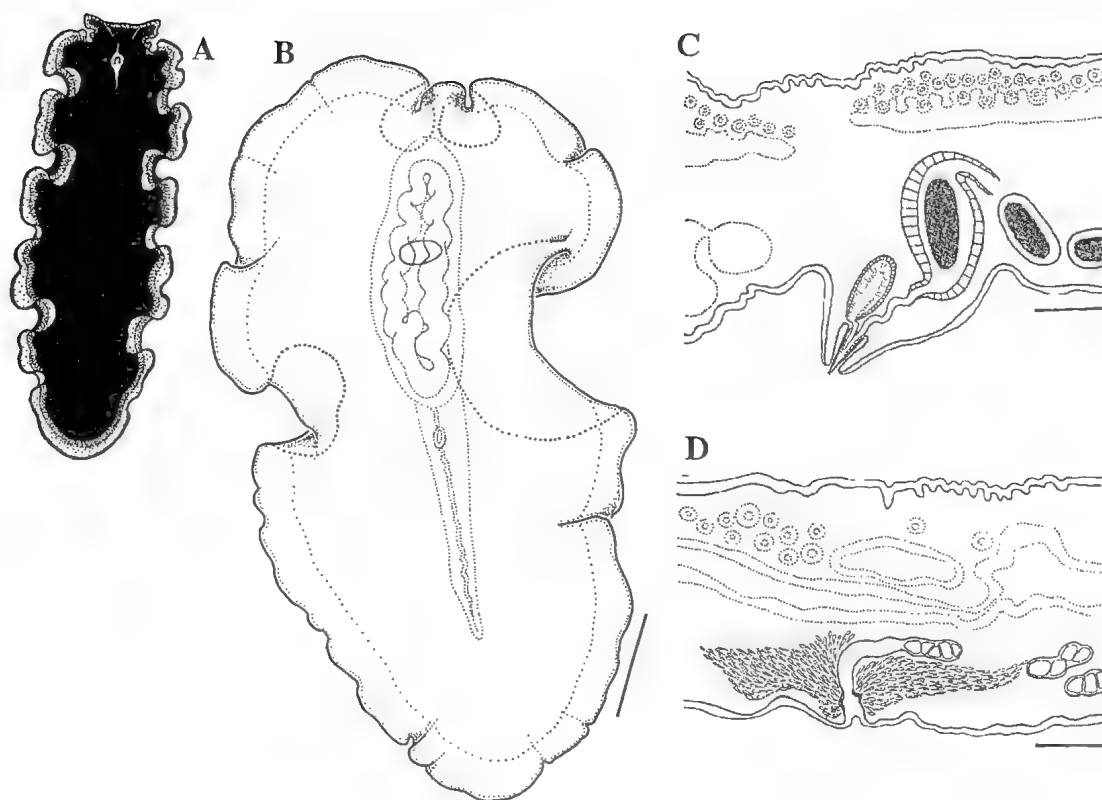


FIG. 37. *Pseudobiceros gloriosus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210549, wholemount showing the morphology from the ventral surface; C, D, QMG210548, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 2.5mm; C, D, 500µm.

orange (165); middle band narrow, pink (223); outer band extremely narrow, dark burgundy (214). Largest specimen with a thin, pink median line beginning at the cerebral eyespot and extending posteriorly to about 3/4 body length. Pseudotentacles with orange and burgundy marginal bands (no pink). Ventrally deep burgundy (214) medially with same marginal bands.

External features. Large species. Pseudotentacles square and slightly ruffled. Cerebral eyespot with about 200 eyes. Two male pores extremely close together. Size: mature from 70 × 25 to 90 × 50mm; juvenile from 28 × 12mm.

Reproductive anatomy. Vas deferens branching. In one system: seminal vesicle oval, large

(1.1µm long); ejaculatory duct long, coiled; prostate elongate, oval (537µm wide); stylet long (463µm). Male and female antra shallow.

DIAGNOSIS

Black with three marginal bands; inner orange, middle pink and burgundy at rim.

ETYMOLOGY

From the Latin *gloriosus* = glorious, for its flamboyant colour pattern.

REMARKS

This species belongs in Group 2 in which the majority of species are black with vibrantly coloured

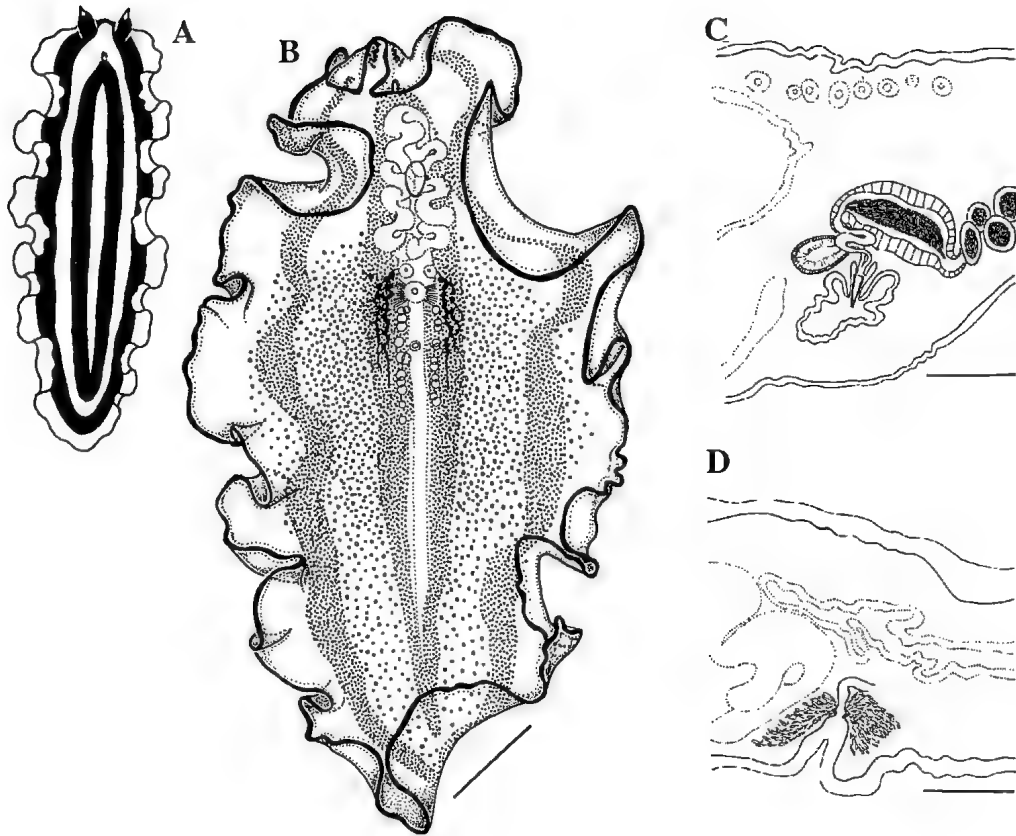


FIG. 38. *Pseudobiceros gratus* (Kato, 1937). A, diagram of the dorsal colour pattern; B, QMG210361, wholemount showing the morphology from the ventral surface; C, D, QMG210566, reconstruction of the reproductive anatomy. C, male system; D, female system. Scales: B, 2.5mm; C, D, 500µm.

marginal bands. *P. gloriosus* has three distinct marginal bands rather than two as found in all other species, except *P. uniaborensis* sp. nov. However, in *P. gloriosus* the marginal bands are orange, purple and violet not orange, grey and white.

HABITAT & DISTRIBUTION

Found under ledges on the reef slope. Common from Heron Is. Rare from Bagabag Is., N Madang. Record: Fiji.

Pseudobiceros gratus (Kato, 1937) (Figs 38 A - D; 51A, B)

- Eurylepta striata* Schmarda, 1859: 27-28, fig. 62.
Pseudoceros striatus (Schmarda, 1859): Stummer-Traunfels, 1933: 3487, 3540, 3544, figs. 95, 96.
Pseudoceros gratus Kato, 1937: 227-229; Kato, 1944: 300; Hyman, 1959a: 566; Prudhoe, 1977: 593-594.
P. strigosus Marcus, 1950: 88.
P. habroptilus Hyman, 1959a, fig. 8.

Pseudobiceros strigosus (Marcus, 1950): Faubel, 1984: 216.

Pseudobiceros gratus (Kato, 1937): Poulter, 1987: 46, pl. 2.1.2.d.

MATERIAL EXAMINED

HOLOTYPE: Unknown, Korôru, Japan [according to Poulter (1975) all Kato's types were lost during World War II].

OTHER MATERIAL: Heron Is., reef slope, 6 - 10m, 27.04.89, S, QMG210562; 30.09.89, WM, QMG210561; 09.09.92, S, QMG210567; 28.01.93, LS, QMG210566; 02.02.93, S, QMG210568; 17.02.93, S, QMG210569; 25.02.93, Müller's larvae, 10 days old, S, QMG210627; One Tree Is., reef crest, 17.08.93, S, QMG210570; Madang, reef crest, 2 - 3m, 08.06.92, LS, QMG210565; WM, QMG210563; 12.06.92, QMG210564.

DESCRIPTION

Colour & pattern. Background varies from transparent white to light brown with three or four parallel thick black (can vary from brown to grey with black borders) lateral stripes, joining posteriorly, extremely narrow black rim. Pseudotentacles black with white tips. Ventral surface transparent white with a narrow black rim.

External features. Body fragile, with deep crenulated marginal ruffles. Pseudotentacles pointed and ear-like. Cerebral eyespot small with about 60 eyes. Size: mature from 40 × 12mm to 50 × 15mm; juveniles from 8 × 6mm.

Reproductive anatomy. Vas deferens branched. In one system: seminal vesicle rounded, oblong (700µm long); ejaculatory duct long, coiled; prostate oval (354µm long); stylet small (158µm long). Male and female antra deep.

REMARKS

This species belongs in Group 3. *P. gratus* is the only species with a white background and appears to be the opposite to *P. philippinensis* which is black with purple-grey stripes.

Confusion has arisen over the synonymy of this species. Schmarda (1859) first named it *Pseudoceros striatus*, a name already occupied by Kelaart, 1858. Kato (1937) named a new species *P. gratus* which proved to be a synonym. Marcus (1950), however, did not recognise the similarities between *P. gratus* and *P. striatus* but renamed Schmarda's species *P. strigosus*. Hyman (1959a) added yet another synonym, *P. habroptilus*, although in the same paper she comments on the previous synonymy of *P. gratus*. However, Poulter (1987) clearly states Hyman's position on the priority of the name *P. gratus*. We accept this here and thus *P. strigosus* becomes a

junior synonym of *P. gratus*, although it remains the type of the genus as designated by Faubel (1984).

Kato (1937) figures the male apparatus of this species which conforms to our specimens whereby the ejaculatory duct is long and coiled, prostate oval, and the seminal vesicle oblong. Details of the female system were not sufficient to compare to our specimens.

BIOLOGY

Eggmasses were laid in containers in the laboratory and Müller's larvae hatched after 10 days.

HABITAT & DISTRIBUTION

Found under boulders from the reef slope and crest. Common from Heron Is. and Madang; rare from One Tree Is. Records: Western Australia, Ceylon, Japan, Micronesia, Hawaii.

Pseudobiceros hancockanus (Collingwood, 1876) comb. nov.
(Figs 39A - D; 51C)

Proceros hancockanus Collingwood, 1876: 91, pl. XVII, fig. 5.

Stylochopsis malayensis Collingwood, 1876: 94, pl. XVIII, fig. 12.

Pseudoceros hancockanus Collingwood, 1876: Laidlaw, 1903: 301, 302, 315; Kaburaki, 1923: 635, 639; Marcus, 1950: 86.

Pseudoceros malayensis (Collingwood, 1876): Bock, 1913: 258, 259.

Pseudoceros hancockanus (Collingwood, 1876): George & George, 1979: 43, pl. 49.

MATERIAL EXAMINED

HOLOTYPE: Not known, painting only?, Singapore.

OTHER MATERIAL: Heron Is., reef slope, 3 - 15m, 21.09.89, WM, QMG210500; 12.90, LS, QMG210501; 02.01.91, S, QMG210502; 21.06.91, WM, QMG210504; 05.09.92, WM, QMG210503; LS, QMG210505; S, QMG210506; 24.02.93, S, QMG210507; One Tree Is., reef slope, 15m, S, 17.08.93, QMG210508.

DESCRIPTION

Colour & pattern. Background velvety black with two distinct marginal bands; inner band wide, orange (151), outer band narrow, white. Pseudotentacles with same marginal bands. Ventral surface grey intensifying to purple medially, marginal bands same.

External features. Largest pseudocerotid recorded. Pseudotentacles square and slightly

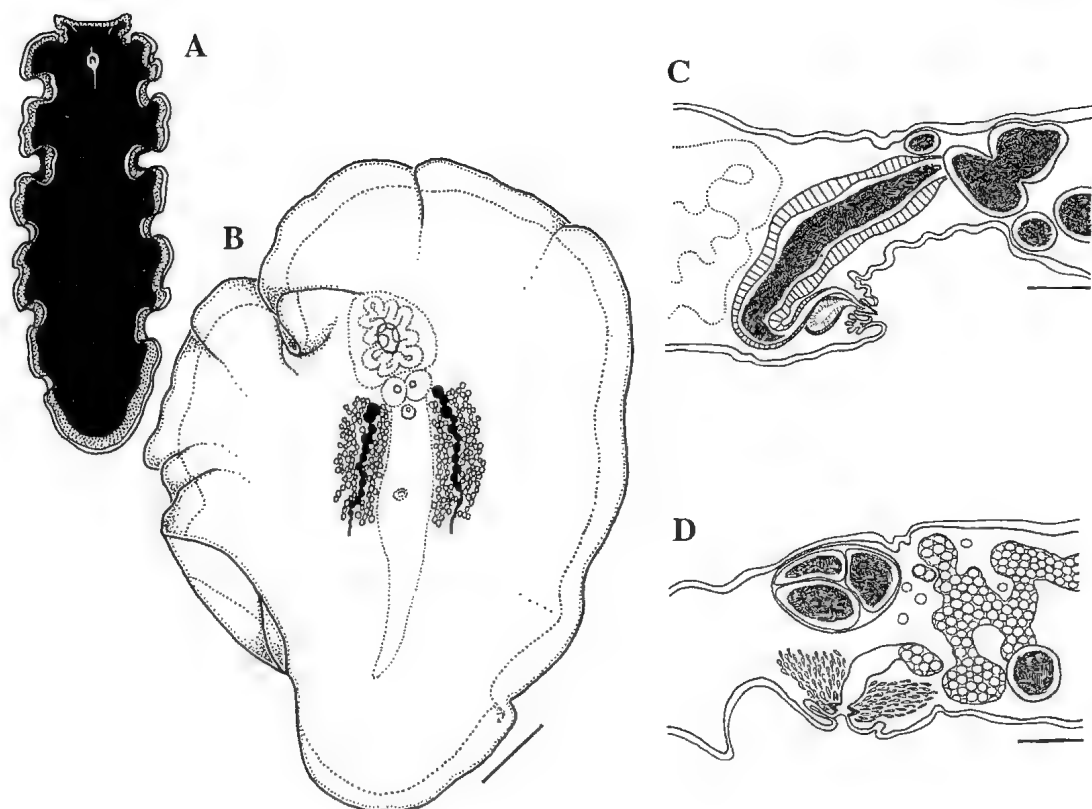


FIG. 39. *Pseudobiceros hancockanus* (Collingwood, 1876) comb. nov. A, diagram of the dorsal colour pattern; B, QMG210507, wholemount showing the morphology from the ventral surface; C,D, QMG210501, reconstruction of the reproductive anatomy. C, one male system, D, female system. Scales: B, 5mm; C, D, 250 μ m.

ruffled. Cerebral eyespot with 100's of eyes. Two male pores well separated. Size: mature from 55 \times 32mm to 140 \times 80mm; juvenile from 4 \times 2mm.

Reproductive anatomy. Vas deferens unbranching. In one system: seminal vesicle elongate, large (1.1mm long), ejaculatory duct short, not coiled; prostate extremely small (175 μ m wide); stylet extremely small (128 μ m long). Male and female antra shallow.

REMARKS

This species belongs in Group 2 where the majority of species possess a black background and vibrantly coloured marginal bands. Only one other species also possesses orange and white marginal bands, *P. uniaborensis* sp. nov.

Proceroshancockanus Collingwood, 1876 was originally described as deep velvety brown with

a double marginal band of equal widths; inner deep orange, outer opaque white. Our specimens clearly possess marginal bands of unequal width. Although no other morphological data were given, we assume that the colour pattern is characteristic for this widespread and common species.

BIOLOGY

One animal was found on an orange sponge and appeared to be feeding.

HABITAT & DISTRIBUTION

Found under ledges on the reef slope. Common from Heron Is. Records: GBR to Laccadives, Japan, Singapore, Philippines.

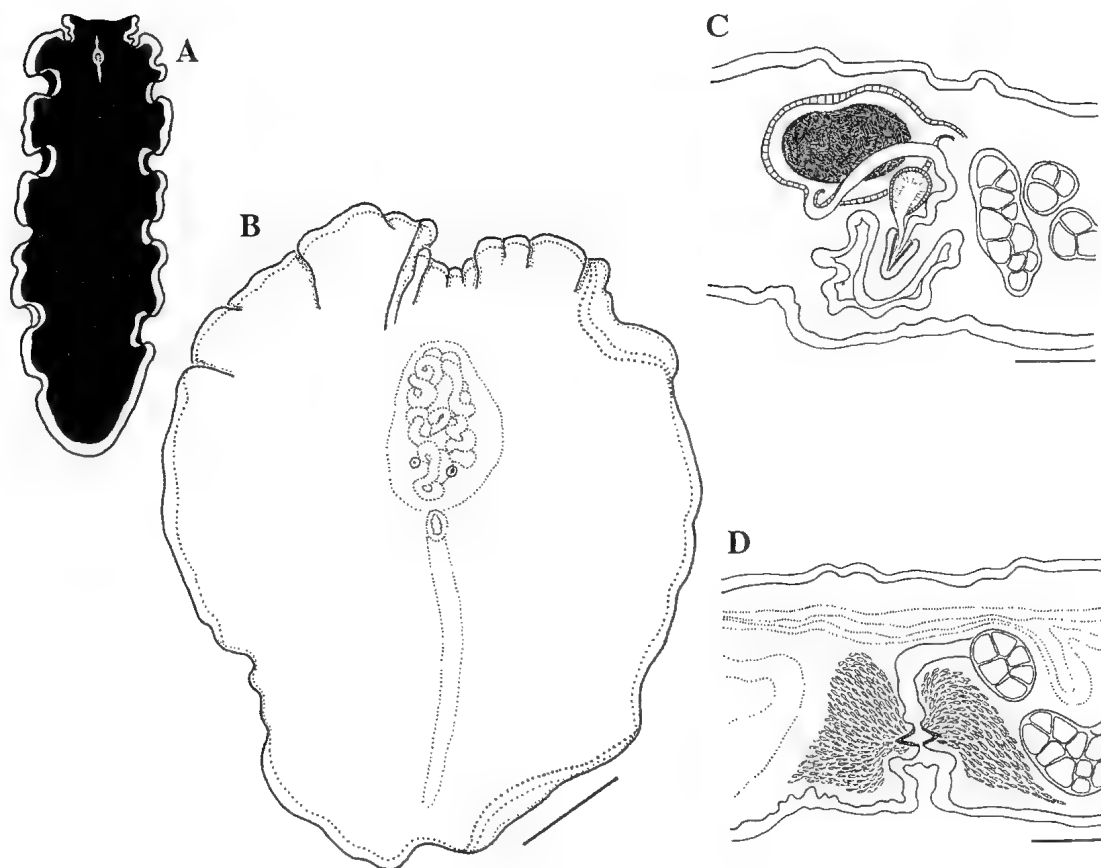


FIG. 40. *Pseudobiceros periculosus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210532, wholemount showing the morphology from the ventral surface; C,D, QMG210535, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 2.5mm; C, D, 250 μ m.

***Pseudobiceros periculosus* sp. nov.**
(Figs 40A - D; 51D)

QMG210530; WM, QMG210531; 04.02.93, S, QMG210534; 17.02.93, S, QMG210533.

? Pseudocerotid Poulter, 1987: 49, pl. 2.I.4 c.

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 12.08.92, WM, QMG210532.

PARATYPES: Heron Is., reef crest, 03.02.92, WM, QMG210526; 20.02.93, LS, QMG210535.

OTHER MATERIAL: Heron Is., reef crest, 17.01.92, WM, QMG210523; 23.01.92, WM, QMG210524; S, QMG210525; 03.02.92, S, QMG210528; 04.02.92, WM, QMG210527; 05.02.92, WM, QMG210529; 07.02.92, WM, QMG210626; 02.08.92, WM,

DESCRIPTION

Colour & pattern. Background velvety black with a wide, distinct, brilliant orange (021) marginal band; extremely narrow colourless transparent rim. Pseudotentacles black without the marginal band. Ventrally grey.

External features. Relatively small species, body with shallow marginal ruffles. Pseudotentacles square and distinctly ruffled. Cerebral eyespot with about 60 eyes. Two male pores well separated. Size: mature from 25 \times 10mm to 30 \times 12mm; juvenile from to 5 \times 2mm.

Reproductive anatomy. In one system: seminal vesicle small, round (570µm long); ejaculatory duct extremely long, coiled; prostate small, oval (175µm wide); stylet small (135µm long), slightly larger than the prostate. Male and female antra deep.

DIAGNOSIS

Black with wide orange marginal band.

ETYMOLOGY

From the Latin *periculosus* = danger, for its black and orange warning colouration.

REMARKS

This species belongs in Group 2 in which the majority of species are black with vibrantly coloured marginal bands, however, only *P. periculosus* possesses a single coloured margin. This species closely resembles *Pseudoceros periauranti* (see above) which is also black with a brilliant orange margin but can be differentiated by its gross morphology. Newman and Cannon (1994) first recognised the similarity of colour pattern between *Pseudoceros* and *Pseudobiceros*. It is assumed that this colour pattern is aposematic.

Laidlaw (1902) originally described *P. flavomarginatus* as velvety-black with an orange margin about 1.5mm wide. No other details were given regarding the shape of the pharynx, eyes or the number of male pores. Therefore, *P. flavomarginatus* is considered incerta sedis as its generic determination is unclear.

DISTRIBUTION

Found on colonial ascidians under boulders at the reef crest. Common from Heron Is. Rare from One Tree Is. Record: Hawaii.

***Pseudobiceros stellae* sp. nov.**
(Figs 41A - D; 51E)

Pseudobiceros sp. Poulter, 1987: pl. 2.I.2 e.

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, on algae, WM, 28.08.89, QMG210633.

PARATYPE: Heron Is., reef crest, on algae, LS, QMG210634.

OTHER MATERIAL: Heron Is., reef crest, 28.12.90, WM, QMG210536; 19.01.92, WM, QMG210537; reef slope, 3m, night, 29.01.92, WM, QMG210538; 29.07.92, WM, QMG210541; WM, QMG210542; night, 30.01.93, S, QMG210540; night, off jetty, P. Lawn, 02.02.93, S, QMG210543; reef crest, 08.02.93, S, QMG210544. One Tree Is., reef crest, 16.08.93, LS,

QMG210545; Madang, reef crest, 3m, 16.06.92, S, QMG210539.

DESCRIPTION

Colour & pattern. Background velvety black or chocolate brown with raised white microdots evenly distributed over the entire surface; larger dots regularly distributed and arranged in 'flower-like' clusters. Pseudotentacles with white tips. Ventral surface blue-black or dark grey.

External features. Pseudotentacles highly developed, square, inflated with deep lateral ruffles. Cerebral eyespot with about 40 eyes in clear oval area. Male pores large, conspicuous and well separated. Size: mature from 50 × 18mm to 60 × 25mm; juveniles from 7 × 4mm.

Reproductive anatomy. Vas deferens unbranched. In one system: seminal vesicle extremely narrow, elongate (667µm long); ejaculatory duct long, coiled; prostate oval (367µm wide); stylet long (244µm long). Male and female antra deep.

DIAGNOSIS

Black with evenly distributed white dots; highly developed, square, ruffled pseudotentacles; extremely narrow and elongate seminal vesicle.

ETYMOLOGY

In honour of the late Mrs Stella Laycock.

REMARKS

This species belongs in Group 4 and only one other species possess a black background colour, *P. bajae*. However, *P. stellae* has regular white dots that form a 'flower-like' arrangement not irregular white dots and highly developed ruffled pseudotentacles. One animal found with two suckers of unequal sizes.

P. stellae is sometimes found under the same boulder as the common nudibranch *Dendrodoris nigra*. Both animals have the same colour pattern, size range and are possibly mimics.

DISTRIBUTION

Found under boulders and out on the rubble at night on the reef crest. Common from Heron Is., rare from One Tree Is. and Madang. Record: Hawaii.

***Pseudobiceros uniarborensis* sp. nov.**
(Figs 42A - D; 51F)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 14.08.92, WM, QMG210599.

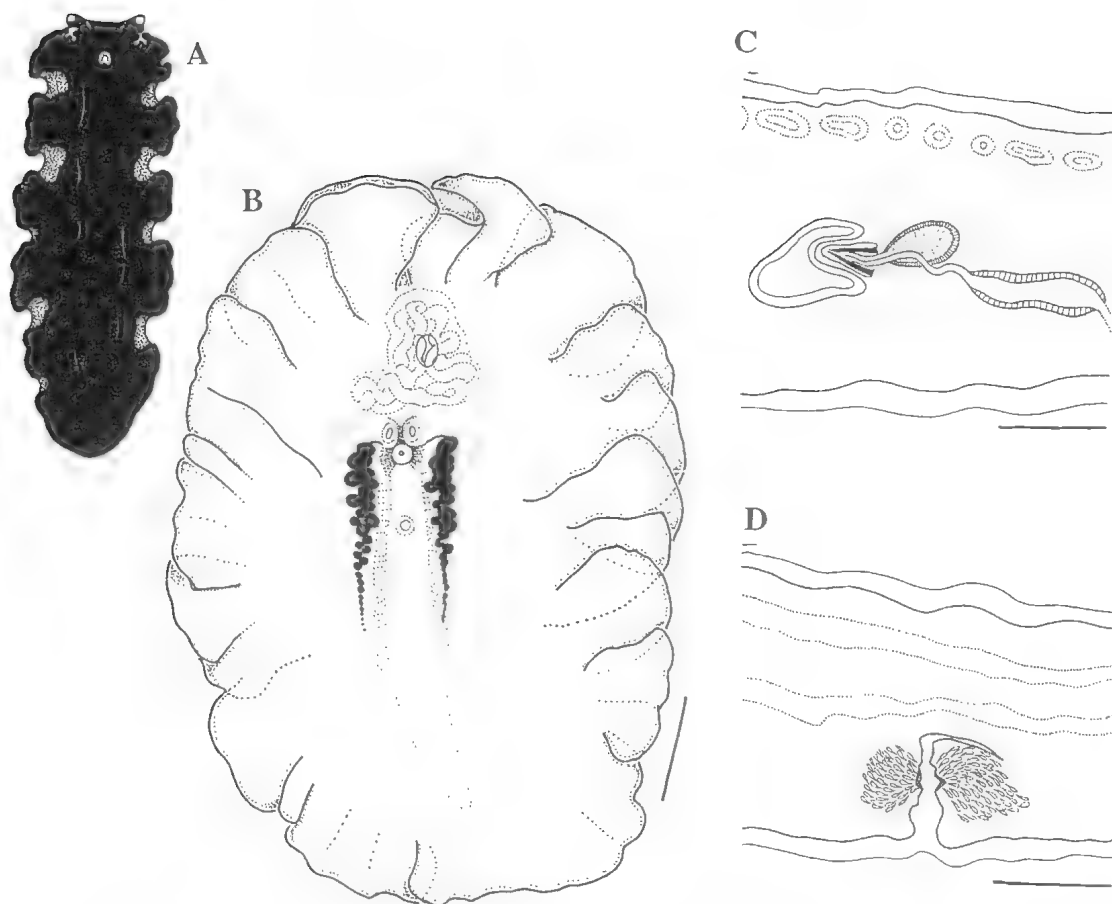


FIG. 41. *Pseudobiceros stellae* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210532, wholemound showing the morphology from the ventral surface; C, D, QMG210535, reconstruction of the reproductive anatomy. C, male system; D, female system. Scales: B, 5mm; C, D, 500µm.

PARATYPE: Heron Is., reef crest, night, 30.01.93, LS, QMG210602.

OTHER MATERIAL: Heron Is., reef crest, 05.02.92, LS, S, QMG210581; 07.02.92, LS, QMG210591; 19.02.92, WM, QMG210592; S, QMG210617; 29.07.92, S, 2 spec., QMG210594; 02.08.92, WM, QMG210595; 07.08.92, S, 2 spec., QMG210596; 11.08.92, S, QMG210597; WM, QMG210598; One Tree Is., reef crest, 13.09.92, S, QMG210600; 11.09.92, LS, QMG210601; 30.01.93, LS, QMG210602; 13.09.92, S, QMG210600; 13.08.93, S, QMG210618. Madang, reef slope, 3m, T. Gosliner, 12.06.92, S, QMG210593.

DESCRIPTION

Colour & pattern. Background velvety black or dark brown: margin with three extremely narrow

bands; inner band bright orange (150 or 137), middle band wide, transparent grey and outer rim opaque white. Pseudotentacles black with white tips but without marginal bands; white-grey triangle between pseudotentacles extending into the cerebral eyespot. Ventrally brown with a white marginal band.

External features. Extremely delicate species. Pseudotentacles pointed and ear-like. Cerebral eyespot with about 60 eyes. Two male pores close together. Size: mature from 55 × 22mm to 60 × 35mm; juvenile from 8 × 3mm.

Reproductive anatomy. Vas deferens branched. In one system: seminal vesicle large rounded oblong (1.39mm long); ejaculatory duct short,

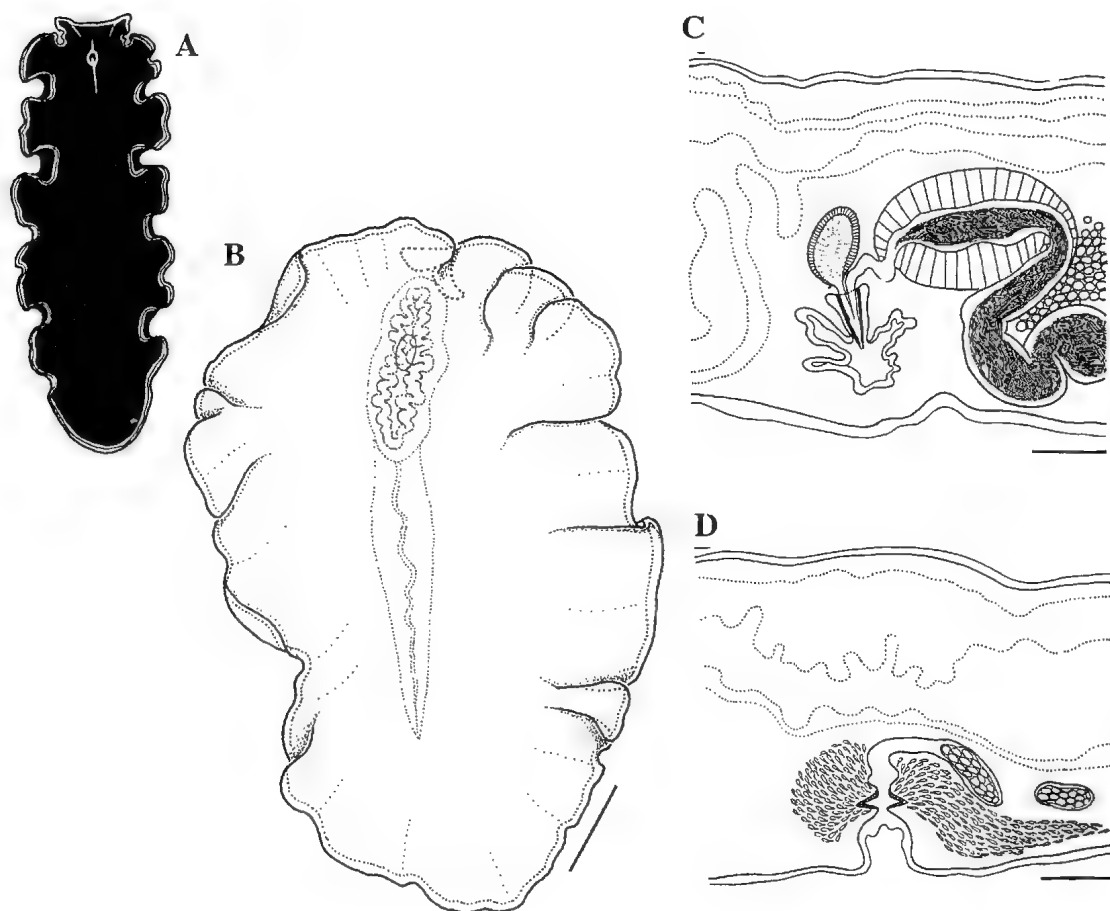


FIG. 42. *Pseudobiceros uniarborensis* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210600, wholemount showing the morphology from the ventral surface; C, D, QMG210602, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 2.5mm; C, D, 500µm.

coiled; prostate large, oval (592µm long); stylet long (389µm long). Male and female antra deep.

DIAGNOSIS

Black with three extremely narrow marginal bands; inner orange, middle grey and white at rim.

ETYMOLOGY

From the Latin *uni* = one, *arborensis* = place of the tree, for the One Tree Island Research Station.

REMARKS

This species belongs in Group 2 and the majority of species are black with vibrantly coloured marginal bands. Only one other species is similar in colour, *P. hancockanus*. However, *P.*

uniarborensis has three narrow marginal bands not two relatively wide bands and pointed ear-like pseudotentacles not square and ruffled pseudotentacles. One animal was found with two suckers.

HABITAT & DISTRIBUTION

Found under boulders at the reef crest and slope. Abundant from Heron and One Tree Is; rare from Madang.

BIOLOGY

FEEDING

Although pseudocerotids are thought to feed on sessile invertebrates, i.e. sponges and ascidians,

there are few reports in the literature. During our study a few feeding observations were made and these indicated that the majority of *Pseudoceros* fed on a variety of ascidian species. One species (*P. bifurcus*) was often observed feeding on a several species of ascidians indicating non-specificity in diet. No other prey was observed being consumed (extended pharynx or feeding scars) although many species were often found crawling or resting on sponges and coralline algae. Crozier (1917) also observed one species (which he called *Pseudoceros* undescribed species, although it appears to be an euryleptid) feeding on three different species of ascidians.

During feeding, animals were often seen in situ with their highly ruffled pharynx expanded into white 'stringlike' projections extended into individual zooids of the colonial ascidians (Fig. 43). Prudhoe (1985) described this feeding behaviour and suggested that when the pharynx is extended a discharge of proteolytic secretions is used to macerate the zooids for digestion. The softened tissue is then supposedly drawn into the intestine which acts as a reservoir while further digestion takes place in the intestinal branches.

Although *Pseudobiceros* were not observed feeding during this study, several animals were collected with large 'lumps' in their intestine. It appears that the feeding behaviour is unlike that found in *Pseudoceros* as described by Prudhoe (1985). Our observations suggest that *Pseudobiceros* engulf prey with the pharynx which can expand to the same size as the animal, secretions from the pharynx may then induce digestion outside the body allowing the pharyngeal muscles to break up the prey which is then sucked, whole, into the intestine.

George & George (1979) reported that a specimen of *Pseudobiceros hancockanus* was found on a sponge and surmised that it was probably searching for small crustaceans inhabiting the sponge's water canals. The same species was also found during this study on an orange sponge and orange granules were found in its intestine suggesting that it was feeding on the sponge itself.

Morphological differences between the pharynx and intestine in the two genera clearly indicate distinct feeding behaviours. Unfortunately, feeding observations were rare and pseudocerotids did not feed in aquaria, possibly due to problems in retaining healthy prey for several days. For most species their prey is unknown.

PREDATION

We do not have direct observations of predation on polyclads. Nevertheless, worms have been seen on several occasions bearing rents and tears in their flesh. Minor tears may be the results of copulatory behaviour (see below), but large tears (presumably bite marks) are thought to be from aborted feeding attempts - we assume by fish. To test this assumption worms were fed to fish in situ and in the laboratory. Although the pieces were readily accepted they were quickly spat out, however, other prey items (i.e. fish, molluscs) were consumed by the fish. These observations suggest worms are distasteful and that their visual predators, fish, would quickly learn to avoid them by recognition of their distinct and bright colour patterns.

COPULATION

Copulatory behaviour in *Pseudoceros* and *Pseudobiceros* was observed for the first time (in situ and in the laboratory) and was recorded on video. During copulation animals were observed to move towards each other, touch, then roll around together, simultaneously everting their penis papillae and stylet(s) outward. They would then try to stab each other anywhere, sometimes causing considerable damage to their partner (Figs 44A, B; 48C, lower animal). On several occasions, both animals reared up and fell towards each other with stylets extended (Fig. 44B). When one animal was successful in penetrating the other, it often held on with its stylet embedded in the epidermis of its partner for up to five minutes and in situ animals often would not let go even if disturbed.

During copulation, loose bundles of white spermatozoa were seen injected in the partner. The sperm could be observed as it moved into the parenchyma in white lines, presumably towards the oviducts. This copulatory behaviour was observed in the laboratory for up to three days with each animal receiving multiple stab wounds. Animals with wounds were able to heal within 24 hours.

LARVAL DEVELOPMENT

When *Pseudoceros* were removed from colonial ascidians under boulders, eggmasses were often observed adhering to the dorsal test of the ascidian. Each irregular shaped eggmass contained a few hundred eggs, tightly packed in a single layer. Eggmasses collected from the field did not hatch in the laboratory.

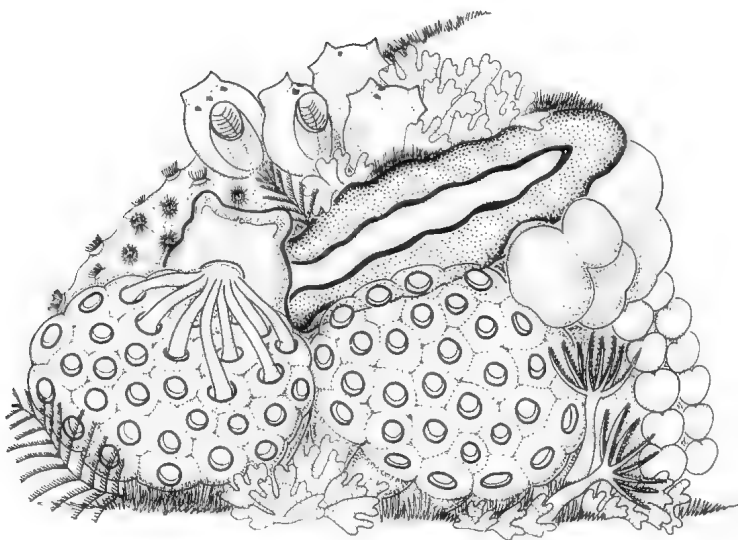


FIG. 43. *Pseudoceros bifurcus* feeding on colonial ascidians by extending sting-like projections of its large ruffled pharynx into individual zooids of the colony.

Pseudobiceros (*P. bedfordi* and *P. gratus*) egg-masses were laid on the side of ice cream containers in the laboratory. These eggmasses were transparent beige becoming darker and more opaque towards hatching, then the developing larvae could be seen moving in the egg cases. Each egg is approximately 75µm maximum diameter. Müller's larvae with their eight lobes (see Hyman, 1951: 174, fig. 67) all hatched on the tenth day of development (Fig. 45) and each measured between 53 - 70µm long. Larvae, although tiny, could clearly be seen swimming in the water column. Larvae from both species were identical; transparent with dark red spots (yolk cells). After six days of development, brown particles could be seen in the digestive gland. Larvae became more streamlined as the lobes were absorbed, swimming in a rolling ciliary motion. During development the lobes continued to be absorbed and the digestive gland grew larger. Larvae tended to cluster together in the surface of the water column only surviving for two weeks after hatching and not settling in this time.

HABITAT & DISTRIBUTION

Members of *Pseudoceros* were the most common polyclads found in the southern GBR (Newman & Cannon, 1994) and displayed the most diverse colour patterns. The majority of species were found on colonial ascidians under boulders

at the reef crest. Many species, although colourful, were actually cryptic when found in situ on their ascidian prey. Some of the most flamboyantly patterned species of both genera (*Pseudoceros ferrugineus*, *P. lindae* and *P. sapphirinus*; *Pseudobiceros gloriosus*, *P. gratus* and *P. hancockanus*) were more often found out and about on or under ledges along the reef slope during the day.

The relatively large size, flamboyant colour pattern and fluid motion of the ruffled undulating margin of *Pseudobiceros* makes them the more conspicuous and

easily observed of the genera. Animals were generally found to be active both during the day and at night. Occasionally, both *P. bedfordi* and *P. hancockanus* were found swimming off the reef crest during the day. Generally *Pseudoceros* were not observed swimming.

Three species were found to be abundant (*Pseudoceros bifurcus*, *P. bolool* and *P. uni-arborensis*) from Heron Island. Few species were found to be abundant or even common at One Tree Island and Madang, but this may be due to the less frequent (and shorter) collecting trips to these locations.

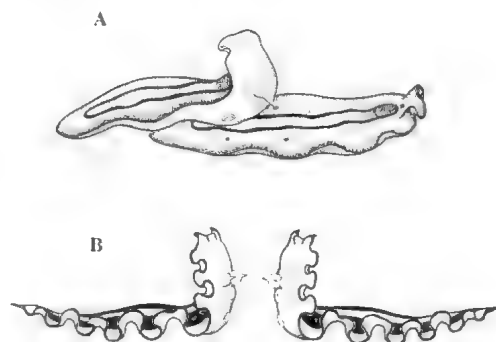


FIG. 44. Copulatory behaviour. A, *Pseudoceros*; B, *Pseudobiceros*.

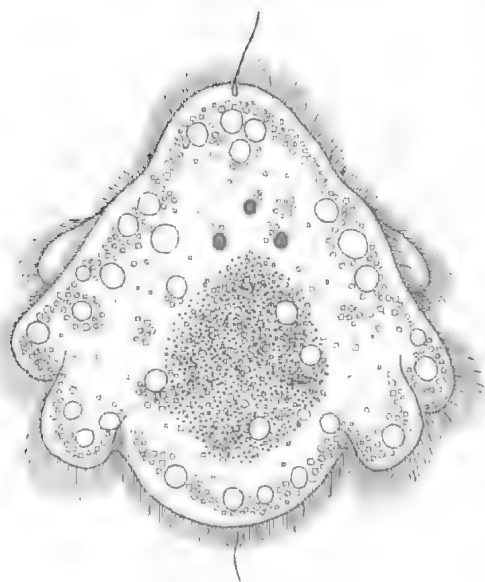


FIG. 45. Müller's larvae of *Pseudobiceros*.

Mimicry between pseudocerotids and toxic phyllidiid nudibranchs has been reported by Gosliner & Behrens (1991) and Newman et al. (1994). During this study two species (*P. bolool* and *P. stellae*) were found to be of similar pattern to the polymorphic nudibranch *Dendrodoris nigra*. This is presumably a further case of mimicry but which animal is the mimic and which the model is not clear as the toxicity of pseudocerotids is yet to be examined.

CONCLUSIONS

We believe that we have demonstrated that the diversity of tropical polyclads belonging to the genera *Pseudoceros* and *Pseudobiceros* is considerable within tropical reefs of eastern Australia and Papua New Guinea. Undoubtedly we have been greatly aided in this research by the development of a reliable fixation procedure for these delicate worms (Newman & Cannon, in press). This aside, we have also shown how vital to the study of these worms is live observation, photography and videography. Criteria of considerable importance which are evident in live study are too often unobserved or totally lost in fixation.

Our observations demonstrate clearly that Prudhoe (1985) was incorrect when he argued for

polymorphism in *Pseudoceros* with regard to the number of reproductive systems. We have shown that a suite of characters (easily seen in live animals) including size, shape, eye arrangement, pseudotentacles, pharynx and topography of the gonopores and sucker all uphold Faubel's (1984) recognition of *Pseudoceros* and *Pseudobiceros* as distinct genera.

We are convinced nevertheless that Prudhoe (1985, 1989) was correct in claiming relative homogeneity within *Pseudoceros* of both the male and female reproductive systems and musculature making determination of species possible on the basis of colour pattern. In this Prudhoe followed Hyman (1954, 1959a) who had also claimed colour patterns were adequate to determine species. Taxonomic problems due to inadequate generic determinations has meant that the number of species belonging to *Pseudoceros* s.s. has been greatly inflated in the past.

We have made a determined effort to provide evidence of homogeneity of the reproductive anatomy by illustrating the sectioned reproductive systems (both male and female) of nearly all species treated, and in so doing have shown camera lucida drawings of the actual sections with, as far as practical, a minimum of interpretative distortion. Our observations, in situ and in the laboratory, of copulatory behaviour provides a convincing explanation for relative reproductive homogeneity. A crude, even savage, intradermal insemination strategy is unlikely to generate elaborate morphological copulatory isolating mechanisms.

Observations did reveal, however, that animals of like patterns copulated simultaneously, mitigating against any argument for polymorphism of colour pattern within species. Further support for species distinctiveness is seen in differences between size at maturity and habitat which indicates that species separated on colour pattern are reliable biological entities. Of course similar or virtually identical patterns have been detected in species in separate genera (cf. *Pseudoceros periauranti* and *Pseudoceros periculosus*) and even separate families (Newman & Cannon, 1994). This reinforces the assertion that though species determination within a genus can rely on colour pattern alone; generic determinations rely on careful morphological analyses. We maintain at this time that serial sectioning of the reproductive structures will be necessary until the limit of criteria needed to determine genera within the family are understood.

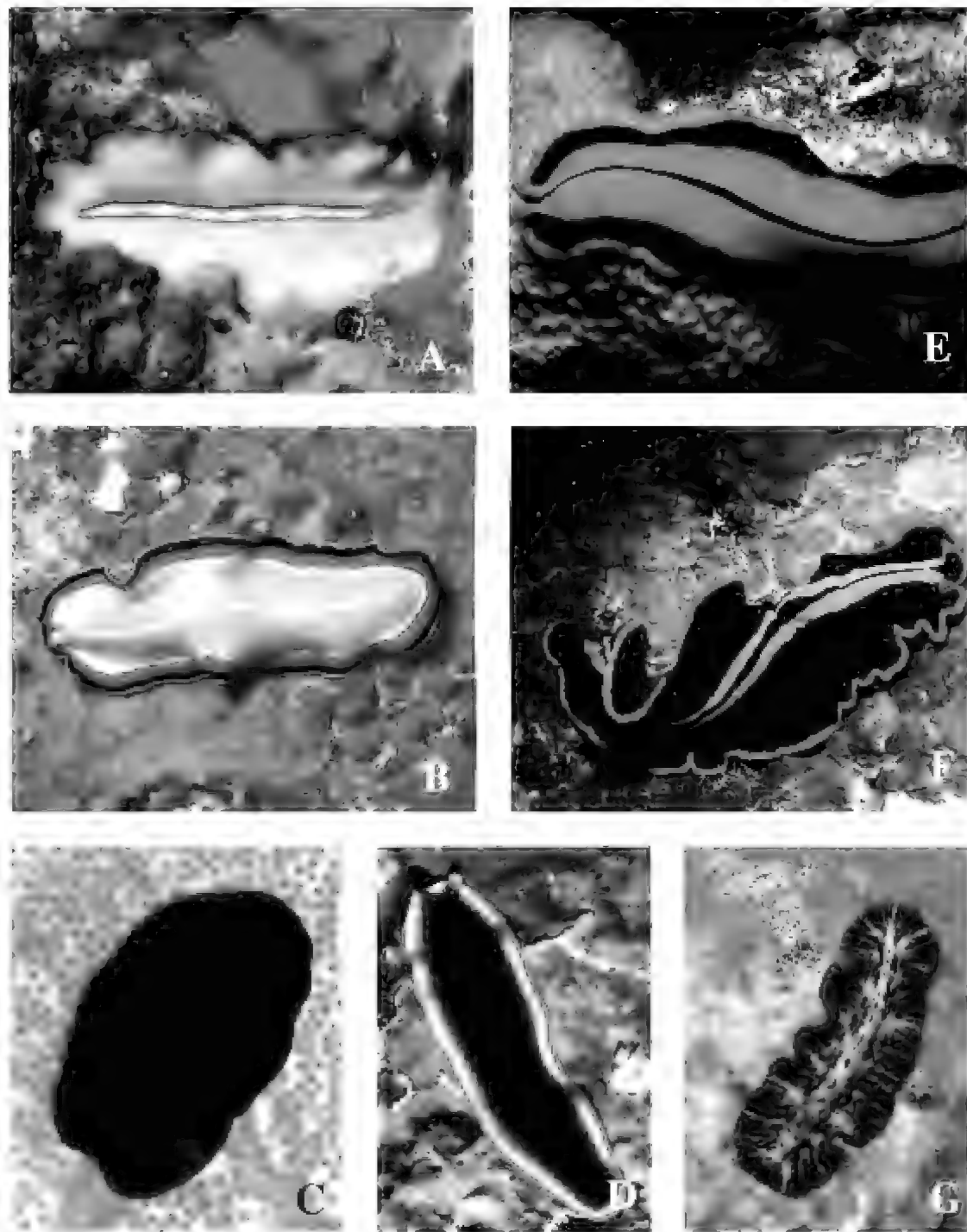


FIG. 46. A, *Pseudoceros bifurcus*, QMG210335, Heron Is.; B, *Pseudoceros bimarginatus*, QMG210381, Heron Is.; C, *Pseudoceros bolool*, QMG210630, One Tree Is.; D, *Pseudoceros depilikitabub*, holotype, Madang; E, *Pseudoceros dimidiatus*, QMG210489, Madang; F, *Pseudoceros dimidiatus*, record only, Madang; G, *Pseudoceros felis*, holotype, Heron Is.

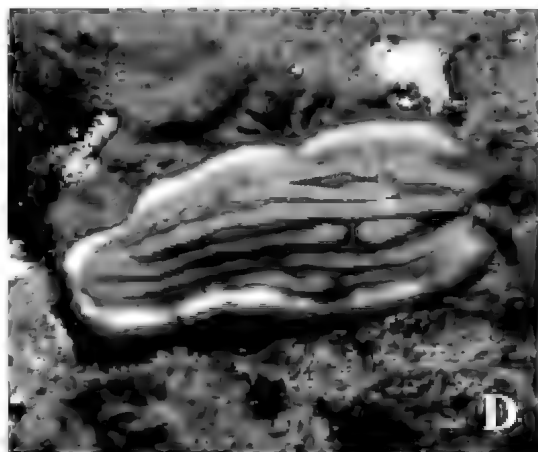


FIG. 47. A, *Pseudoceros ferrugineus*, QMG210368, Heron Is.; B, *Pseudoceros goslineri*, QMG210452, Heron Is.; C, *Pseudoceros gravieri* juvenile, QMG210345, Heron Is.; D, *Pseudoceros gravieri* adult, GBR (photo only G. Allen); E, *Pseudoceros heronensis*, QMG210461, Heron Is.; F, *Pseudoceros jebborum*, QMG210469, Madang.

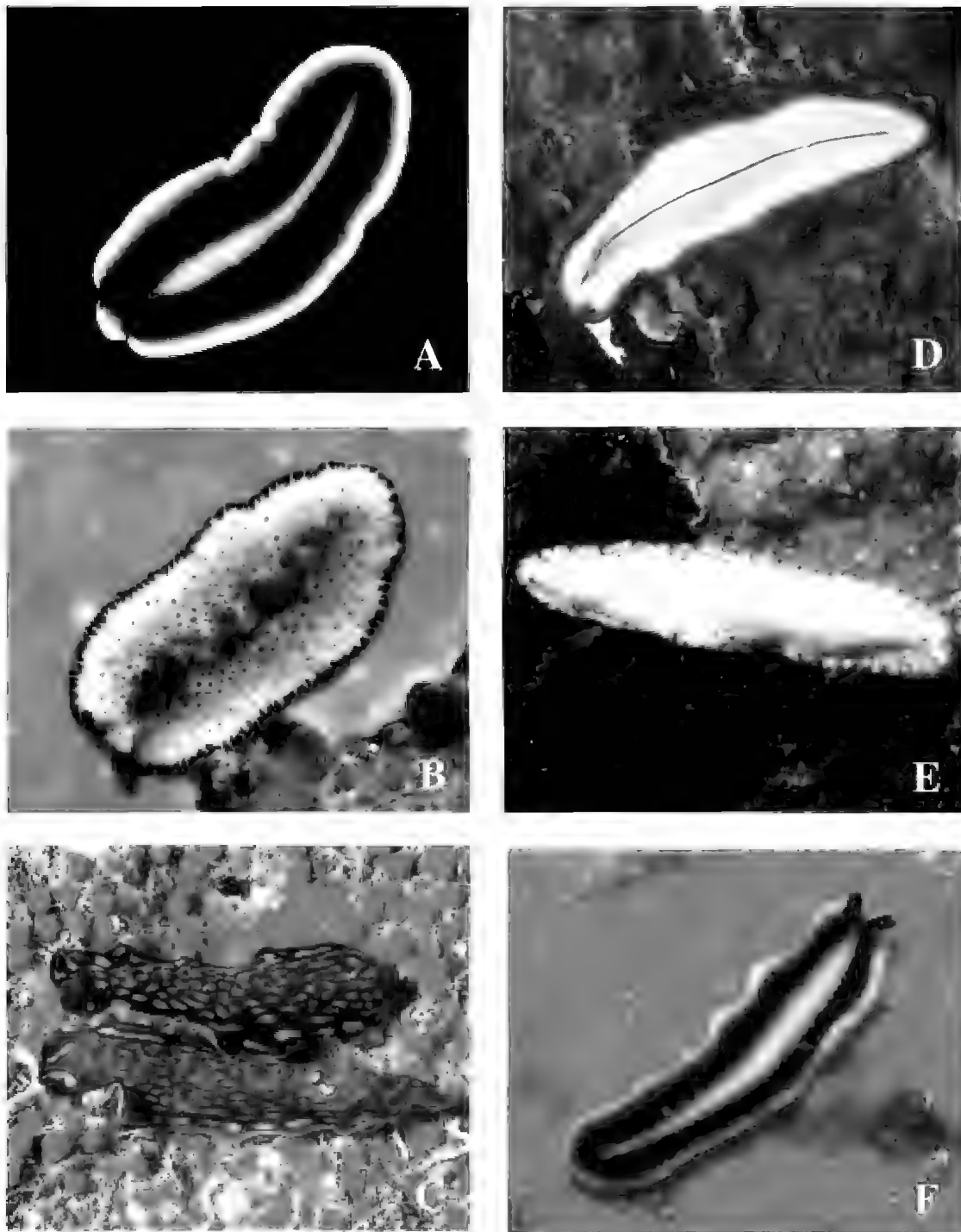


FIG. 48. A, *Pseudoceros laticlavus* (record only), Heron Is.; B, *Pseudoceros leptostictus*, QMG210341, Heron Is.; C, *Pseudoceros lindae*, holotype, Heron Is.; D, *Pseudoceros monostichos*, holotype, Heron Is.; E, *Pseudoceros ouini*, holotype, Madang; F, *Pseudoceros paralaticlavus*, paratype, QMG210428, Heron Is.

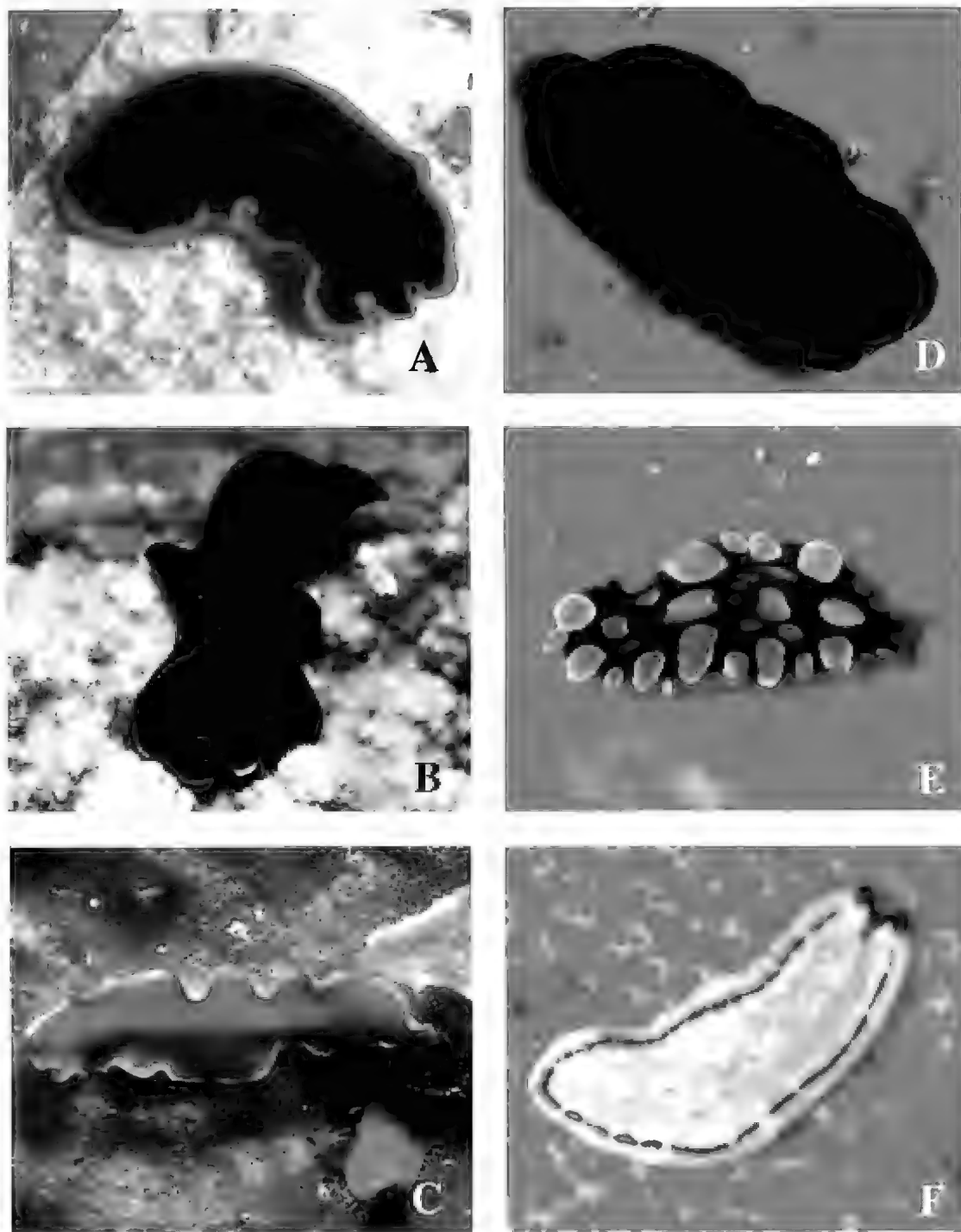


FIG. 49. A, *Pseudoceros periaurantius*, paratype, Heron Is.; B, *Pseudoceros peripurpureus*, holotype, Heron Is.; C, *Pseudoceros prudhoei*, paratype, QMG210402, Heron Is.; D, *Pseudoceros sapphirinus*, QMG210522, One Tree Is.; E, *Pseudoceros scintillatus*, holotype, Heron Is.; F, *Pseudoceros vercundus*, QMG210499, One Tree Is.

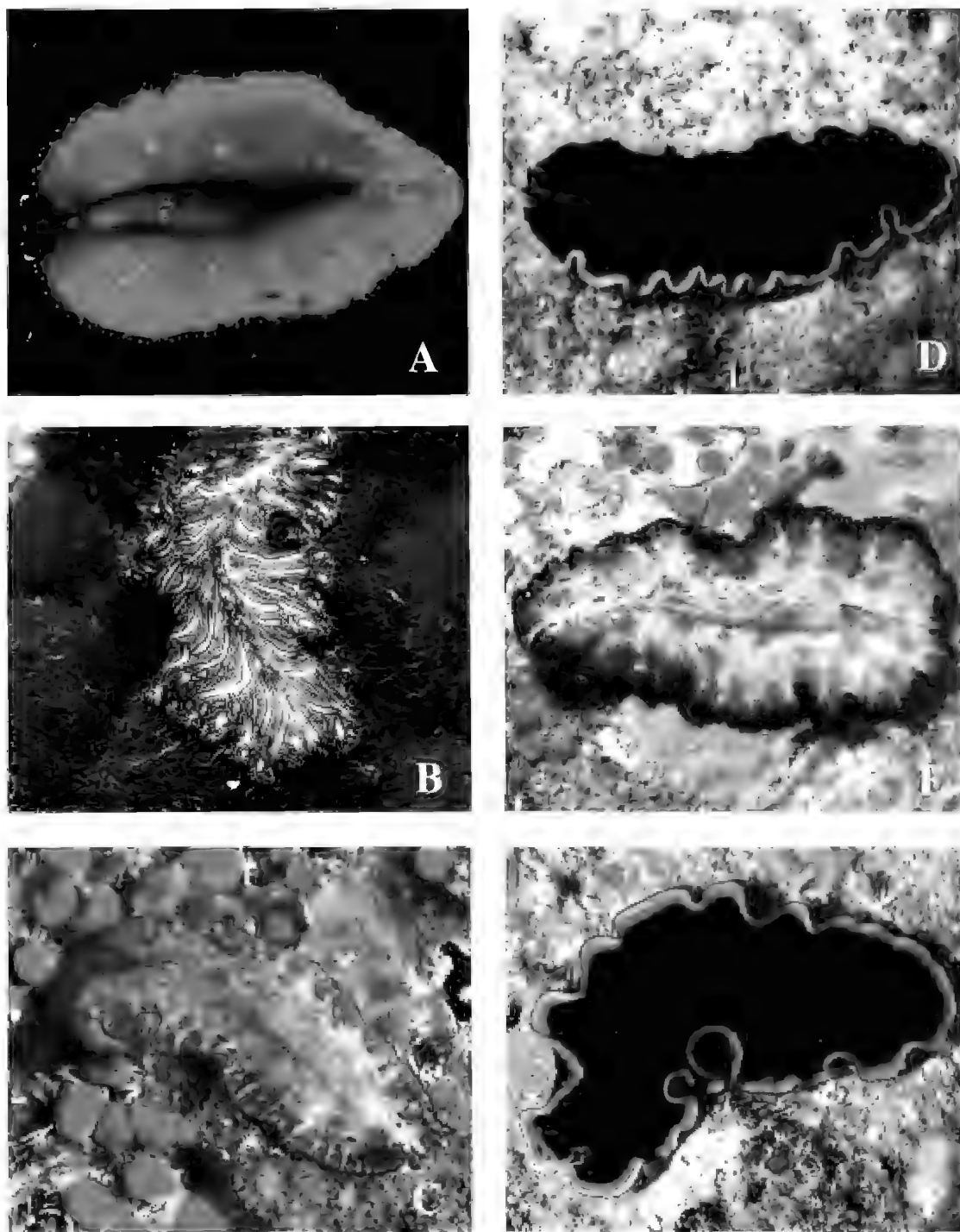


FIG. 50. A, *Pseudobiceros apricus*, QMG210571, Heron Is.; B, *Pseudobiceros bedfordi* (record only), Heron Is.; C, *Pseudobiceros damawan*, QMG210611, Heron Is.; D, *Pseudobiceros flavocanthus*, paratype, Madang; E, *Pseudobiceros fulgor*, paratype, QMG210556, Heron Is.; F, *Pseudobiceros gloriosus*, QMG210551, Heron

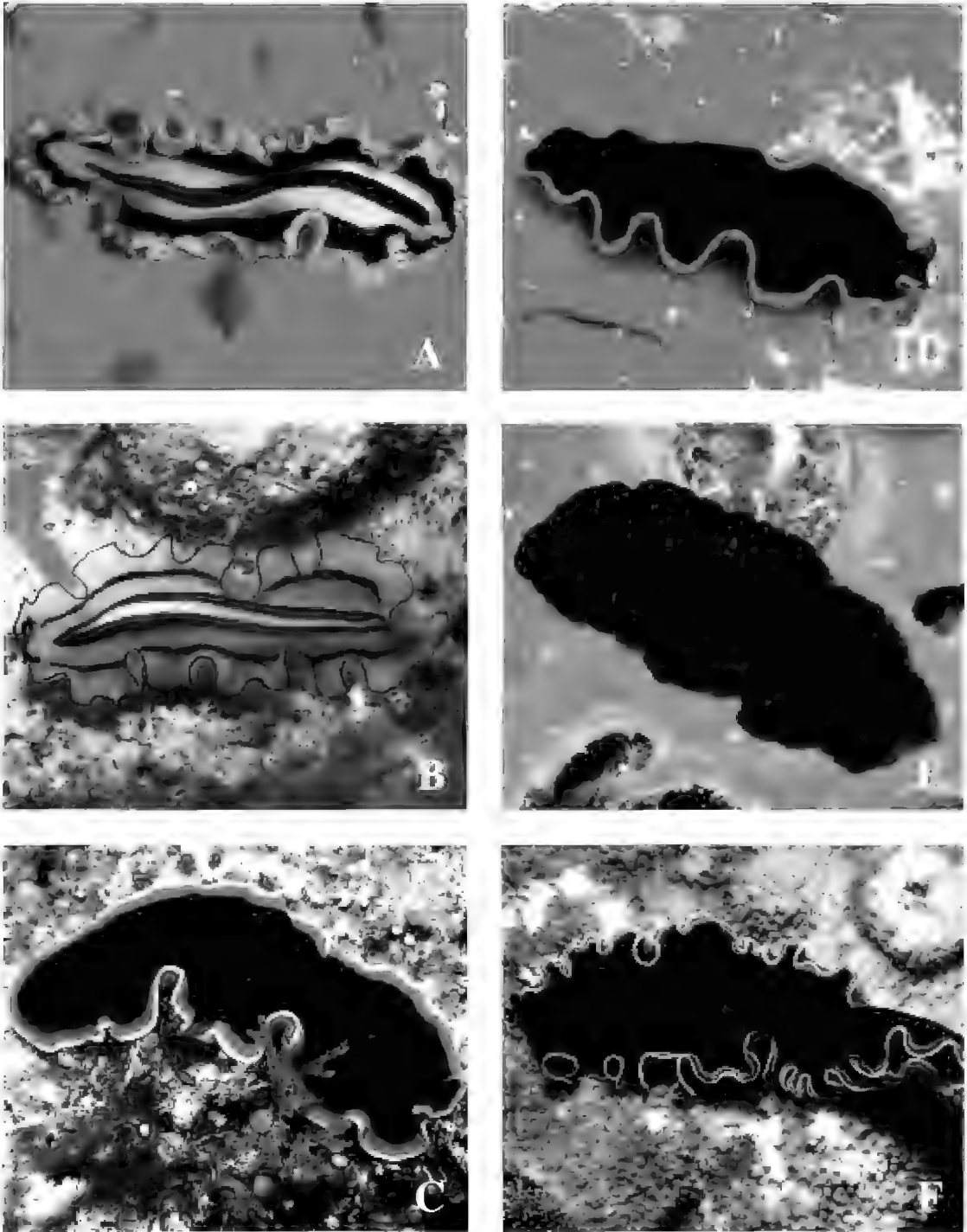


FIG. 51. A, *Pseudobiceros gratus*, QMG210570, One Tree Is.; B, *Pseudobiceros gratus*, QMG210564, Madang; C, *Pseudobiceros hancockanus*, QMG210508, One Tree Is.; D, *Pseudobiceros periculosus*, paratype, QMG210535, Heron Is.; E, *Pseudobiceros stellae*, holotype, Heron Is.; F, *Pseudobiceros uniaborensis*, paratype, Heron Is.

The taxonomic implications of our study are that without critical morphological details which allow a generic determination, many species in *Pseudoceros* sensu lato simply cannot be placed. By confirming the validity of *Pseudobiceros* and by examining descriptions of *Pseudoceros* s. l. in the light of our emended diagnoses we can reliably place only a limited number of species in these two genera. Other species may be placed within these genera following re-examination and careful recollection at their type localities.

We have attempted to standardise the description of colour patterns in pseudocerotids. First, we have adopted the Pantone standard for reliable colour recording. Secondly we have provided a vocabulary to describe colour patterns and finally we have erected six pattern groups to contain species. We are conscious that this is a first attempt and anticipate further refinement as more species are found and described.

We cannot believe the colours patterns are meaningful to the species in any intraspecific visual sense. Some are clearly warning colours, some serve to mimic other species (Newman et al., 1994) and some are clearly cryptic. Therefore colour pattern appears to be a specialised anti-predation strategy. In the reef environment we must assume the primary visual predators of polyclads are fish. Our observations clearly suggest that scarred worms are tasted but not consumed by fish (wounds usually heal within 24 hours). Evidence from trials of worms fed to reef fish, in situ, and in the laboratory (Newman & Flowers, unpub. obs.) indicated that fish readily accept, but immediately reject, polyclad flesh. These observations strongly suggest an anti-predatory nature to the chemistry of these worms.

Flamboyant colour patterns (aposematism) would serve to warn fish of the flatworm's distastefulness (toxicity) and dull colour patterns would provide camouflage (Newman et al., 1994). It should be noted that our perception on the quality of a colour pattern depends entirely on the habitat of the flatworm. A brilliantly coloured animal may be cryptic on a similarly coloured background (e.g. colonial ascidian) and hence there is a need to study these animals live and in situ.

The presence of aposematic colour patterns suggests that chemical defences are significant deterrents to predation. Chemicals must also be significant in precopulatory behaviour. Copulatory mechanisms are crude so presumably recognition must rely on chemical means since

visual cues are discounted. The elaboration of the anterior margin into large pseudotentacles is further evidence that these worms rely substantially on chemosensory mechanisms to determine their behaviour. We believe these flatworms offer a rich field of research for marine chemists and fish ethnologists.

ACKNOWLEDGEMENTS

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TWO NEW SPECIES OF BROODFROGS (*PSEUDOPHRYNE*) FROM QUEENSLAND

G.J. INGRAM AND C.J. CORBEN

Ingram, G.J. & Corben, C.J. 1994 12 01. Two new species of broodfrogs (*Pseudophryne*) from Queensland. *Memoirs of the Queensland Museum* 37(1): 267-272. Brisbane. ISSN 0079-8835.

Pseudophryne raveni sp.nov. from southeast to mideast Queensland is most similar to *P. coriacea*, with which it probably hybridises. However, it can be readily distinguished by its different advertisement call and colouration. *P. covacevichae* sp.nov. from northeast Queensland is most similar to *P. major* but differs in colour pattern and breeding season. □ *Pseudophryne, raveni, covacevichae, coriacea, major, hybrid, new species, broodfrog, Myobatrachidae, Queensland, Australia.*

G.J. Ingram & C.J. Corben, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 10 February 1994.

For many years it has been known that there were two sympatric species of *Pseudophryne* in southern Queensland: *P. major* Parker, 1940 was a winter breeder and *P. coriacea* Keferstein, 1868, a summer breeder (Ingram, 1983). However, there is uncertainty in the literature about the identity of the taxon *P. major* and how it differs from *P. bibronii* Günther, 1858 (e.g. Ingram & Corben, 1975; Cogger, 1992; Tyler, 1992). Unfortunately, we do not have the information to address this problem in this paper. From our observations, however, there is little doubt that the taxon presently called *P. major* in southern and central Queensland is a valid species but we are unsure of the southern extent of its range and thus unsure of its correct name. This is because what is called *P. bibronii* in New South Wales is a complex of new and described species. Until the taxonomy of that species is elucidated in southern Australia, the names *P. major* and *P. bibronii* will be doubtfully used. As well, there is a formal, nomenclatural problem with the latter: Cogger et al. (1983) noted that the only surviving specimen of the four syntypes of *P. bibronii* is a *P. guentheri* Boulenger, 1882.

In Queensland, what has been called *P. major* consists of more or less continuous populations in central and southern Queensland and several isolated populations in far northern Queensland (Ingram & Raven, 1991: fig. 101). In this paper we describe the Atherton Tableland population as a new species (*P. covacevichae*) and comment on a record from Cape York Peninsula. Since 1974, we have been aware of two forms of *P. coriacea* in southern Queensland that differ in mating call and colour pattern, and which apparently hybridise. We describe the northern coastal form as a new species, *P. raveni*.

Abbreviations follow Ingram & Corben (1990). Specimens prefixed by 'QMJ', 'AMR' and 'BMNH' are housed in the Queensland, Australian and Natural History Museums respectively. Measurements are in millimetres and ratios are expressed as percentages; those of the holotypes are given in square brackets.

Pseudophryne covacevichae sp.nov. (Fig. 1)

MATERIAL EXAMINED

HOLOTYPE: QMJ52286, Millstream Falls NP, adjacent to park entrance, 5.2 km W of Ravenshoe, NEQ (145°22'30"E, 17°38'30"S), K.R. McDonald, M. Davies, G.F. Watson, 27 January, 1991.

PARATYPES: QMJ53870, QMJ53920-32 Ravenshoe, 5 km W; AMR104460, AMR104463 Ravenshoe?

DIAGNOSIS

Distinguished from all other *Pseudophryne* by the bright rufous brown to yellow dorsal colouring that forms a connected cap and vertebral stripe, which terminates in a yellow line that inserts into a yellow cloacal patch. Further distinguished from *P. major* (Fig. 1) in breeding behaviour (*P. covacevichae* breeds in spring to summer and *P. major* in winter and autumn).

DESCRIPTION

SV 24-28 (N 17, mean 26.3) [25]; TL/SV: 30-35 (N 17, mean 33.0) [30]; HW/SV: 26-33 (N 17, mean 29.0) [29]; HW/TL: 82-100 (N 17, mean 87.6) [87]; ED/HW: 35-45 (N 17, mean 41.3) [38]; IN/EN: 81-96 (N 17, mean 89.9) [91].

Dorsal ground colour bright rufous brown to yellow with diffuse, black paravertebral lines; thus the frog appears to have a bright cap and vertebral stripe. Cloaca surrounded by a large

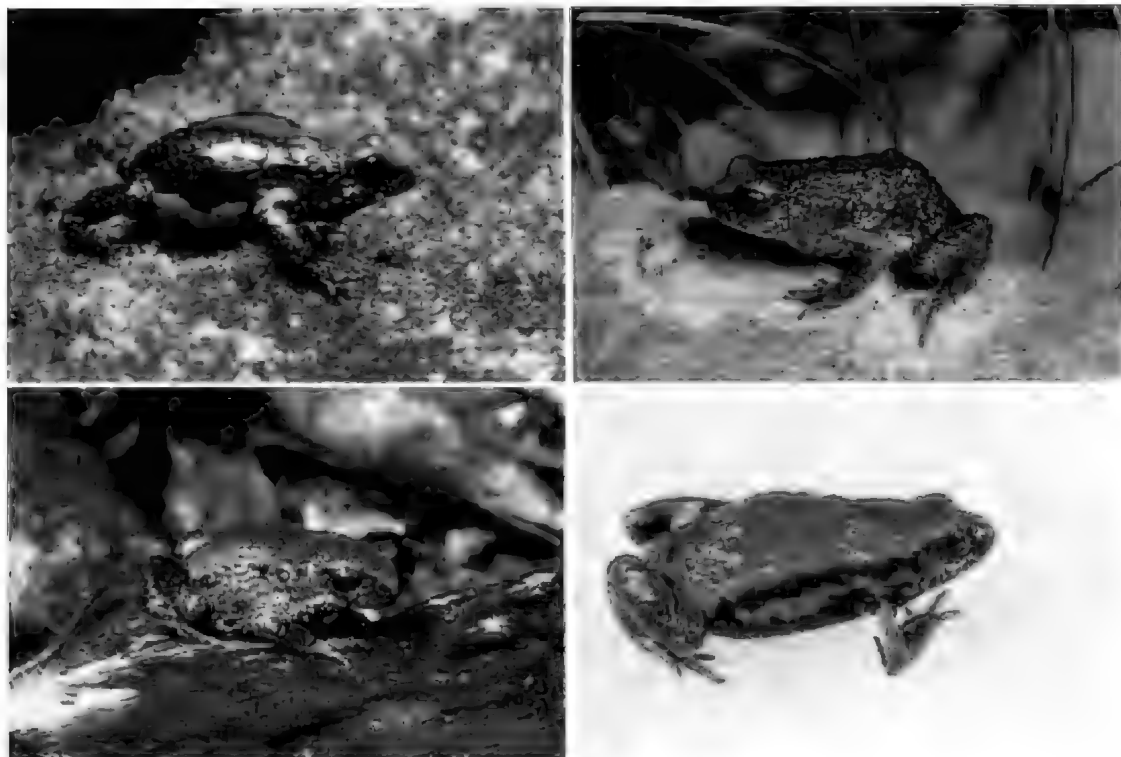


FIG. 1. Top left: *P. covacevichae* sp. nov., holotype, QMJ52286, Millstream Falls NP, NEQ. Top right: *P. major* Parker, 1940, Boondall, Brisbane, SEQ. Bottom left: *P. raveni* sp. nov., paratype, QMJ58434, Woogaroo Ck nr Wacol, SEQ. Bottom right: *P. coriacea* Keferstein, 1868, New South Wales.

yellow patch, which extends upwards as a thin, yellow vertebral line connecting with the dorsal ground colour. Sides of body black, sometimes suffused with white or grey. Dorsal surface of upper arm bright yellow. Ventrally boldly marbled in black and white. Upper half of iris yellow to gold in adults.

DISTRIBUTION

Known only from open forest in the Ravenshoe area, NEQ: Millstream Falls National Park and the adjacent Timber Reserve 245, and Ravenshoe dump (K. McDonald & S. Richards, pers. comm.).

REMARKS

P. covacevichae appears to be most similar to *P. major* and, to the ear, the calls are indistinguishable. However, the latter is a winter breeder while *P. covacevichae* breeds in summer. We have not examined the holotype of *P. major* Parker, 1940, but we have studied photographs of it, which are in the possession of Mr Keith Mc-

Donald. From our examination, we concluded that the holotype (listed as BMNH1947.2.20.24 by Cogger et al., 1983), with its uniform ground colour on the dorsal and lateral surfaces of the body ('brown' in Parker, 1940), was a member of the taxon traditionally identified as *P. major* in southern Queensland (e.g. Ingram, 1983; Morley, 1991). We did not examine the specimens of Woodruff (1976), which, at least in part, will be *P. covacevichae*.

In the maps of Ingram & Raven (1991: fig.101), *P. covacevichae* was included with *P. major*. Also included was a record from much further north, on Cape York Peninsula. This record was based on two specimens QMJ12952-3 from Wenlock donated by W.J. Fisher. The material had no date of collection but was registered at the Queensland Museum on 31 July 1951. The record was reluctantly included in Ingram & Raven (1991) because it was suspected that the locality was in error (Ingram, pers. comm.). However, the locality appears to be correct. These specimens were given by Fisher to Donald P. Vernon (then

of the Queensland Museum) while Vernon was on the Archbold Expedition of the American Museum of Natural History in 1948 (Vernon, pers. comm.). The expedition was at the Wenlock during 10-28 July 1948 (Brass, 1953) – Vernon from 24-28th. Vernon further told us that he should have been collecting only birds at the time because Brass (the expedition leader) had forcibly told him earlier (at Mt Tozer) not to collect any other animal groups. However, Vernon had been sent by George Mack, the Director of the Queensland Museum, with specific orders to collect all groups. But, because Vernon was the only Australian and a guest of the Americans, he felt he had little choice but to obey Brass. Even so, he did accept several herpetological specimens from the Fisher family while at Wenlock.

Unfortunately, even though the collection locality appears to be correct, Fisher's *Pseudophryne* specimens are in poor condition and we could not classify them. Any decision about their specific status will have to await the collection of new material. Even so, they are smaller than most individuals of other Queensland species and appear to be adult.

Where exactly Fisher's specimens were collected could be a problem. However, Vernon (pers. comm.) said Fisher ran a mine quite close to the Wenlock River crossing.

ETYMOLOGY

For Ms Jeanette Covacevich. The common name 'Magnificent Broodfrog' is recommended for *P. covacevichae*.

OTHER MATERIAL

P. major: QMJ1359-70, White Mts NP; QMJ50626-9, Collaroy Holding; QMJ49259-60, Croydon Rd, 16.4km from St Lawrence turnoff; QMJ51575-83, QMJ51587-9, St Lawrence turnoff, 16.4km along Croydon Rd; QMJ31787-9, airport clearing, Shoalwater Bay Army Res; QMJ53168-9, QMJ53201-3 Shoalwater Bay Army Res, Wadallah Ck; QMJ53210, Shoalwater Bay Army Res; QMJ10408-9 Mt Etina; QMJ19812, QMJ19823, QMJ19840 Emu Park Rd, c.26km NE of Rockhampton; QMJ43166, Frenchville; QMJ48113-5, North Rockhampton; QMJ42710-2, Curtis Is; QMJ50616-7, Curtis Is, nr Turtle St beach, on rd going inland; QMJ34202-3, halfway up escarpment, Blackdown Tbl; QMJ28506-7, QMJ47648, QMJ50804-6, Blackdown Tbl; QMJ34298, Mimosa Ck, Blackdown Tbl, via Dingo; QMJ50659-61, Blackdown Tbl, rd to Rainbow Falls; QMJ39128-30, QMJ39132-3, QMJ39135, Blackdown Tbl, via Duaringa; QMJ55022, Mt Larcom; QMJ50633-5, Mt Zarnia, c.3km N Springsure; QMJ37759-60, Mt Zarnia;

QMJ55018, Dan Dan SF; QMJ40314, Deepwater Rd, S of Town of 1770; QMJ40110-1, Kroombit Tops, 2nd causeway, Ubobo Rd; QMJ56036, Bunbuncundoo Spring Ka Ka Mundi NP; QMJ53079, Consuela Tbl; QMJ42685-7, QMJ42689, Gin Gin Ck, 4 miles upstream from Gin Gin; QMJ16667, Gin Gin Ck, Gin Gin; QMJ16666, Gin Gin; QMJ55196, Bania SF 54, Monto; QMJ53080-1, Mt Moffat NP, Lethbridge Pocket; QMJ42224-5, Mt Moffat NP, track to Kennifs Lookout; QMJ50601, Carnarvon Gorge, Carnarvon NP; QMJ19818, QMJ19820-1, QMJ19992, 34km S of Bundaberg; QMJ50615, Robinson Gorge NP, gorge bottom; QMJ46031-2, Punchbowl Ck, 25km N of Columboola; QMJ296, Eidsvold, Burnett R; QMJ617, QMJ12646-65, Eidsvold; QMJ18067, 3km W of Gayndah; QMJ18068, Dawson R crossing, Carnarvon Hwy; QMJ55195, Deep Ck, Timber Reserve 581, Biggenden; QMJ19831, c.11km SW of Maryborough; QMJ18070, 13km S of Ban Ban Springs; QMJ40440, QMJ40514, Cooyar; QMJ55467-8, Boogooramunya SF 643; QMJ39193-4, Byanda Stn, 20km NNW of Proston; QMJ18069, 8km W of Goomeri; QMJ40439, Imbil; QMJ1103, Buderim Mtn; QMJ50658, Jimna SF, Marumba Ck; QMJ30888, 1km E of The Breadknife, Booloomtha Ck, Conondale Ra; QMJ50643, Bellthorpe SF, Conondale Ra, Sandy Ck; QMJ40441, Crum-hurst; QMJ42697-8, QMJ42700-9, QMJ42713, c.5 miles E of Rockwood, Candamine-Kogan Rd; QMJ19792, QMJ19833, Bunya Mtns; QMJ40515-6, Kilcoy; QMJ19805, 11km N of Caboolture; QMJ40992, Eagers Swp, Moreton Is; QMJ29262, Beachmere; QMJ42519-21, N end of Redcliffe Golf Course; QMJ50607, QMJ50613-4 Crows Nest NP; QMJ19837, QMJ19848, Samsonvale; QMJ21429, Bald Hills, Brisbane; QMJ10405, Boondall, Brisbane; QMJ10499, QMJ10524-5, QMJ10903-4, Samford; QMJ42684, Mt Nebo Rd, Mt Nebo; QMJ12861, Enoggera, Brisbane; QMJ19830, Fernvale; QMJ566, Kelvin Grove, Brisbane; QMJ98, QMJ106, QMJ1503, QMJ2214, QMJ2421, QMJ2424-5, QMJ2435-9, QMJ12667, QMJ12851-2, Brisbane; QMJ42692, West Ihaca Ck, Brisbane; QMJ2444, Toowong, Brisbane; QMJ42681-3, Lake Manchester, just below dam; QMJ19799, QMJ19806-7, QMJ19809, QMJ19836, Lake Manchester Rd, 6km W of Mt Crosby; QMJ56819, Mt Crosby, cnr Wattle & Belah Court; QMJ19808, 6km S of Fernvale; QMJ14473-6, Brookfield, Brisbane; QMJ15903, QMJ19793-8, QMJ19811, QMJ19827, QMJ19832, St Lucia, Brisbane, Munroe St Swamp; QMJ19800-4, QMJ19813, QMJ19819, QMJ19825-6, QMJ19834-5, QMJ19841, Lake Manchester Rd, 3km from Mt Crosby; QMJ42679, Seven Hills State School, Seven Hills, Brisbane; QMJ19814, QMJ19845, Kenmore; QMJ10380-1, Yeerongpilly, Brisbane; QMJ116, Toowoomba; QMJ15911-2, QMJ15914, Moggill Farm, Brisbane; QMJ12791-4, Sunnybank, Brisbane; QMJ42696, Calam Rd, Runcorn; QMJ10434, Runcorn, Brisbane; QMJ42678, QMJ42680, QMJ42688, QMJ42690, QMJ42695, QMJ42699, Kingsley St, Rochdale; QMJ19817, QMJ19822, Grandchester Rd,

SE of Laidley; QMJ19791, QMJ19828-9, Ipswich-Boonah Rd, 6km from New England Hwy junct; QMJ19842, QMJ19844, Flinders Peak Rd; QMJ19815-6, QMJ19838, QMJ19843, QMJ19846, 3km S of Tamborine Village; QMJ42693, Numinbah Valley; QMJ19810, Numinbah Valley Rd 3km past Numinbah Valley T-junction; QMJ42694, Lost World; QMJ42623-4, QMJ50636, Girraween NP, camping ground.

Pseudophryne raveni sp.nov.

(Fig. 1)

MATERIAL EXAMINED

HOLOTYPE: QMJ58433 Woogaroo Ck nr Wacol, SEQ (27°36'S, 152°54'E), Ric Natlgrass, 20 February, 1994.
PARATYPES: QMJ56789, Pinnacle, NW of Mackay, Teemburra Dam site; QMJ43850-1, Eungella; QMJ55194, Byfield NP; QMJ55021, Mt Larcom; QMJ55019, Dan Dan SF; QMJ42220, N of Eurimbah NP, via Miriam Vale; QMJ49439, Agnes Waters Rd, 3 miles W of Agnes Waters; QMJ40176, QMJ1959, Bindarac Stn, 10km ENE of Miriam Vale; QMJ42763-4, Callide Ck, Kroombit Tops; QMJ40141-9, Kroombit Tops, 2nd causeway, Ubobo Rd; QMJ42757, Barracks, Kroombit Tops; QMJ42749, QMJ42751-3, Three Moon Ck, Kroombit Tops, 45km SSW of Calliope; QMJ42158-9, QMJ42186, Kroombit Tops; QMJ42760-2, Lower Dry Ck, Kroombit Tops; QMJ27949, Warro, nr Lowmead; QMJ23855-6, slopes of Mt Warro SF, 16km SW of Lowmead; QMJ30085, Kenfield Farm, Deepwater Ck nr Wreck Rock; QMJ39268, Lake Coomboo, Fraser Is; QMJ18729, 3km W of Childers; QMJ50656, Churchill Mine Rd, 6.5km along rd, from Maryborough; QMJ50655, Hervey Bay road, 12.8km along rd, from Maryborough; QMJ35801-2, Ferguson, via Maryborough; QMJ35803-4, Black Spring, Maaroom, via Bauple; QMJ35805-6, Magnolia, Tuan SF; QMJ23952, QMJ27483, Como Scarp, Cooloola; QMJ42643-51, Cooloola, swamp nr Teewah Ck; QMJ29990-1, Lake Coolamerra, 6.4km W, Cooloola; QMJ42652, Lake Coolamerra, Cooloola NP; QMJ27399-402, Cooloola NP, via Gympie; QMJ18718, 2km S of Pomona; QMJ42677, Noosa R, Harry Springs Hut; QMJ31881, Yabba Stn; QMJ29277, Jiggera Scrub, c.15km N of Jimna; QMJ31886-9, 10km N of Jimna; QMJ32209, Booloumba Ck headwaters, Conondale Ra; QMJ52285, Jimna; QMJ1506, Buderim Mtn; QMJ30882, 1km E of The Breadknife, Booloumba Ck, Conondale Ra; QMJ40443, QMJ40518, QMJ42671 Conondale Ra; QMJ50630, QMJ50637-42, QMJ50644-54, Bellthorpe SF, Conondale Ra, Sandy Ck; QMJ54402-5, Conondale Ra, 30m from Booloumba Falls Car Pk; QMJ35108, QMJ40445-6, QMJ40517, Maleny; QMJ18716, Bruce Hwy, 45km S of Nambour; QMJ29278-9, Kilcoy; QMJ18707, Lake Manchester Rd, 6km W of Mt Crosby; QMJ29259, QMJ29263, Beachmere; QMJ19824, Samford; QMJ18717, QMJ34160-1 Mt Nebo; QMJ42668-9, Mt

Nebo Rd, Mt Nebo; QMJ18699-700, QMJ18702, QMJ18704-5, QMJ18709, QMJ18711-3, QMJ18720-1, QMJ18723, QMJ18725, Mt Glorious Rd, 10km from Stafford; QMJ12304, QMJ12310, The Gap, Brisbane; QMJ1505, QMJ12867, Brisbane; QMJ18719, St Lucia, Brisbane, Munroe St Swamp; QMJ42656, QMJ42660 West Ithaca Ck, Brisbane; QMJ18726, Orchard Tce, St Lucia, Brisbane; QMJ42653-4, QMJ42657, Cleveland Rifle Range, Cleveland; QMJ18708, QMJ18710, Lake Manchester Rd, 3km past Mt Crosby; QMJ37032-3, Rochedale; QMJ42655, QMJ42658-9, QMJ42661-7, QMJ42691; Kingsley St, Rochedale; QMJ30878, QMJ40442, QMJ40444, Mt Cotton; QMJ40214-5, QMJ40258, Stretton, Brisbane; QMJ12385, Acacia Ridge; QMJ2955, Goodna Scrub; QMJ57286, Bellbird Park, Devon Crt; QMJ58434, Woogaroo Ck nr Wacol; QMJ36902, QMJ37470, QMJ37543, Daisy Hill SF; QMJ40519, Mt Tamborine; QMJ18722, Eagle Heights-Palm Grove; QMJ27449, QMJ27451, QMJ27453, Nerang turnoff 1km from Gold Coast Hwy; QMJ50632, Rathdowney.

DIAGNOSIS

Distinguished from other species of *Pseudophryne* by its relatively long, drawn out advertisement call and, except for *P. coriacea*, by its reddish dorsal ground colour. In colouration, *P. raveni* is most similar to *P. coriacea* but, with the latter (Fig. 1), the sides of the body are evenly black, often with bright red to reddish brown patches enclosed by the black (vs black to dark brown dorsolateral stripe with lower lateral surface reddish brown suffused with black or grey).

DESCRIPTION

SV 14-28 (N 141, mean 23.0) [25]; TL/SV: 26-41 (N 141, mean 36.1) [36]; HW/SV: 27-40 (N 141, mean 32.4) [29]; HW/TL: 77-108 (N 141, mean 90.0) [89]; ED/HW: 24-40 (N 141, mean 32.4) [32]; IN/EN: 68-98 (N 141, mean 83.1) [86].

Dorsal ground colour, red to reddish brown to coppery, sometimes with a blackish lyre-shaped marking, but usually with a broad darker, vertebral stripe. Upper lateral surface of the body, black to dark brown, usually forming a dorsolateral stripe, which may break up into dots towards the hindlegs. Lower lateral surface reddish brown suffused with black or grey. Dorsal surface of upper arm same colour as dorsal ground colour. Ventrally, boldly marbled in black and white. Upper half of iris coppery in adults.

DISTRIBUTION

From near Nerang, SEQ, north to the Eungella Region, W of Mackay, MEQ. *P. raveni* apparent-

ly hybridises with *P. coriacea* around the base of the Scenic Rim, SEQ.

REMARKS

P. raveni is a frog of open forests preferring soaks and springs and not swamps. It breeds during the warmer months from September to March, apparently mutually exclusive with the breeding period of sympatric *P. major*, which is a 'winter' breeder. The advertisement call is a drawn out ratchet sound that speeds up and rises in pitch at the end of the call, finishing sharply. The call of *P. coriacea* is a ratchet sound too. However, it is about a third the duration of *P. raveni*'s call (and does not speed up and rise in pitch) and, to the ear, is indistinguishable from *P. major* and other eastern Australian *Pseudophryne*.

As with sympatric populations of *P. coriacea* and *P. bibronii* in New South Wales (White, 1993), no hybrids of *P. raveni* and *P. major* have been found. However, *P. raveni* apparently intergrades with *P. coriacea* in southeast Queensland. In the one zone of overlap so far discovered (near Nerang, SEQ), combinations of the two call types can be heard. Such zones need further investigation to discover if the two species are actually hybridising. However, we have not located any other areas where the two species overlap: much of their habitat has been cleared for agriculture and housing developments.

ETYMOLOGY

For Dr Robert Raven. The common name 'Copper-backed Broodfrog' is recommended for *P. raveni*.

OTHER MATERIAL

Pseudophryne coriacea: QMJ50606, Crows Nest NP; QMJ42670, QMJ42672-6, Ravensbourne Rd, 15 miles W of Esk; QMJ50608-12, Ravensbourne NP; QMJ42629, Governors Chair, Spicers Gap; QMJ50602-4, Lamington NP, Binna Burra; QMJ50631, Springbrook; QMJ29969-75, QMJ29995-9, Mt Lindesay Hwy, 11.2 km N of border; QMJ27442, QMJ27448, QMJ27454, 39 km towards Numinbah from Nerang turnoff; QMJ42637-42, Girraween area, Storm King dam Rd; QMJ42626-8, QMJ42630-6, QMJ50605, Girraween NP area; QMJ29984, QMJ29986-8, Murwillumbah, 11.2 km S; QMJ27450, Mt Lindesay Hwy, 2 km S of border; QMJ29959-63, QMJ29976-9, QMJ29980-2, Mt Lindesay Hwy, 4.8 km S of border; QMJ27452, Mt Lindesay Hwy, 13 km S of border; QMJ29968, Murwillumbah, 10.4 km S; QMJ29983, QMJ22985 Murwillumbah, 11.2 km S; QMJ18706, QMJ18714-15, QMJ18727, Lismore Rd, 32 km SW of Murwillumbah; QMJ45495, Rosebank,

via Lismore; QMJ18728, Lismore; QMJ29992-4, QMJ27443, QMJ27446, QMJ27490, Ballina; QMJ56814, Tabbimoble SF, SW Ballina; QMJ39222, Gibraltar Ra; QMJ42619-22, Gibraltar Range NP, Mulligans Hut track; QMJ55252-3, Oakwood SF; QMJ55256, QMJ55260 Brother SF; QMJ55254-5, Glen Nevis SF; QMJ28223-4, Cooplacurripa, 25 km NW; QMJ46387-401, Pillar Valley, c. 25 km E of Grafton; QMJ18701, Putty Rd, Colo Heights; QMJ46403-34, Bulahdelah, c. 15 km S on Pacific Hwy; QMJ56395, Myall Lakes, nr Bulahdelah.

P. raveni × *P. coriacea*?: QMJ27976-91, Nerang turnoff 13 km towards Numinbah Valley; QMJ27444, QMJ27457, Nerang turnoff 15 km from Gold Coast Hwy; QMJ27445, QMJ27455, Nerang turnoff 16 km from Gold Coast Hwy; QMJ29964-7, Nerang turnoff 16.6 km from Gold Coast Hwy.

ACKNOWLEDGEMENTS

We thank Keith McDonald (Queensland Department of Environment and Heritage) for the opportunity to examine his photographs of the holotype of *P. major* and for collecting the holotype of *P. covacevichae* for photography. Similarly, we thank Ric Natrass (Queensland Department of Environment and Heritage) for collecting the holotype of *P. raveni*. Gary Cranitch, Queensland Museum, took the photographs. We also thank Ross Sadler (Australian Museum) for access to specimens in his care and Mike Trenerry of Cairns for the opportunity to hear a tape of the call of *P. covacevichae*. Mr Don Vernon kindly agreed to be interviewed about his time with the American Museum of Natural History's expedition to Cape York Peninsula.

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A NEW SPECIES OF *LITORIA* (ANURA: HYLIDAE) FROM NEW GUINEA AND A REDEFINITION OF *LITORIA LEUCOVA* (TYLER, 1968)

G.R. JOHNSTON AND S.J. RICHARDS

Johnston, G.R. & Richards, S.J. 1994 12 01. A new species of *Litoria* (Anura, Hylidae) from New Guinea and a redefinition of *Litoria leucova* (Tyler, 1968) *Memoirs of the Queensland Museum* 37(1): 273-279. Brisbane, ISSN 0079-8835.

At present *Litoria leucova* is known from the holotype collected at Busilmin near the north flowing May River and seven specimens from the south flowing Ok Tedi in the Star Mountains of New Guinea. We show that the specimens from the north and south faces of the central mountains represent two distinct species. This paper describes the southern taxon as *Litoria majikthise* sp. nov. and redefines *L. leucova* confining it to the northern taxon. □
Hylidae, Litoria leucova, Litoria majikthise, new species, New Guinea.

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Litoria leucova (Tyler, 1968) was described from a single adult female collected from Busilmin near the May River on the northern slopes of the Star Mountains of Papua New Guinea. Menzies (1993) redescribed the species based on seven specimens from the south flowing Ok Tedi, without reference to the holotype, and placed it in the *Litoria nigropunctata* species group.

During field work in the Western and Sandaun Provinces of Papua New Guinea we collected specimens which, after comparison with type material, made it clear that *L. leucova* as defined by Menzies (1993) is polytypic. The specimens Menzies (1993) referred to *L. leucova* are not this species but represent an undescribed species. In this paper we report further specimens of *L. leucova* and describe and illustrate the new species.

MATERIALS AND METHODS

Eight morphometric measurements (in mm) were made of specimens of *Litoria iris*, *L. leucova* and the new species held in the South Australian Museum (SAM) and the University of Papua New Guinea (UPNG). These measurements were: snout-vent length (SVL), head width (HW), head length (HL), eye diameter (ED), eye to naris interval (EN), internarial span (IN), tibia length (TL) and foot length (FL) following Tyler (1968).

Descriptive statistics and a number of morphometric ratios were calculated from these measurements. All measurements and proportions given are for adult males unless otherwise stated. A discriminant function analysis (Rey-

ment, et al., 1984) was done to test for significant multivariate differences in raw measurements between the three taxa.

Calls were recorded in the field with a SONY Professional Walkman cassette recorder and an Electret Condenser microphone ECM Z200. Calls were analysed using ULTRASOUND v1.10 (Jordan, 1988).

COMPARISONS

Litoria leucova was originally diagnosed on the basis of a single female with: 1, SVL = 30.4mm; 2, an immaculate blue dorsum and stippled blue on the thighs; 3, an eye to naris distance less than internarial span; 4, no vomerine teeth; 5, an immaculate unpigmented ventral surface; 6, no flash markings in the groin or on posterior surfaces of thighs; and 7, unpigmented ova (Tyler, 1968). This specimen was collected on the northern slopes of the Star Mountains.

The specimens Menzies (1993) referred to as *L. leucova* were all male and quite different from the holotype: they were larger (SVL = 31.0-35.4mm), mottled on the dorsum, had bright red flash markings in the groin and on the hidden surfaces of the thighs, large purple patches on the ventrolateral surfaces, and possessed vomerine teeth. All of these specimens were from the southern slopes of the Star Mountains.

Since the holotype was female and all of Menzies' (1993) specimens were male, these differences may have reflected sexual dimorphism in one species. However, this is unlikely for a number of reasons. Firstly, male Anura are usually smaller than females. The existence of a species with a reversal of this pattern would be

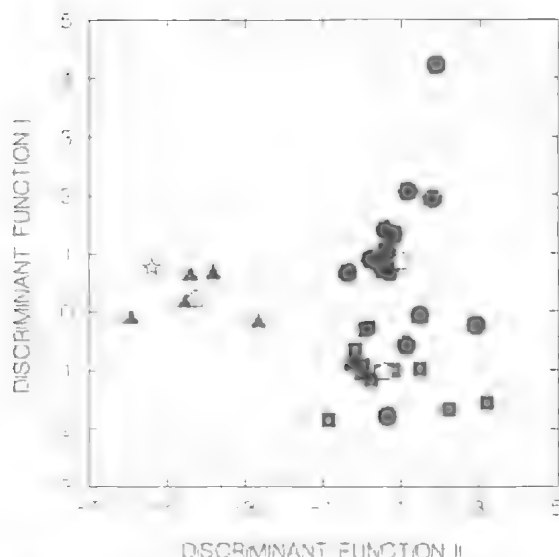


FIG. 1. Plot of individual *Litoria iris* (circles), *Litoria leucova* (triangles) and *Litoria majikthise* (squares) on the first two discriminant function axes based on seven measurements. Hollow pentagons = group centroids. Hollow star = holotype of *Litoria leucova*.

very unusual, especially in the absence of morphological or behavioural indications that male combat is important in this species (Shine, 1979). Secondly, we have collected a female of the 'southern' taxon and found it to be larger than males (SVL=39.2mm) but entirely consistent with them in all other respects. Thirdly, several males collected near the type locality of *L. leucova* correspond in all respects to the holotype of that species, but differ from males of the southern taxon in morphology and structure of the mating call.

Thus, two separate taxa, from the southern and northern slopes of the Star Mountains, appear to be included in Menzies' (1993) concept of *L. leucova*. This hypothesis was tested using a discriminant function analysis of seven measurements using *L. iris*, the southern and northern *L. leucova* as a priori groupings (Fig. 1). *L. iris* was included in this analysis because phenetically it is the species of *Litoria* most similar to the southern taxon.

There were two significant discriminant functions, the first of which accounted for 81.4% of the variance. All measurements contributed significantly to decrease Wilk's Lambda. The analysis resulted in correct identification of 93.8% of specimens overall. All *L. iris* and northern *L. leucova*, and 85.7% of southern

L. leucova were correctly identified. All misidentified southern frogs were assigned to the group representing *L. iris* by the analysis. A posteriori placement of the type specimen of *L. leucova* onto the discriminant functions demonstrated clearly that it falls within the northern cluster, but well outside of the clusters representing *L. iris* and the southern taxon. On the basis of this morphological analysis and differences in mating call we describe the southern *L. leucova* as a new species, and redefine *L. leucova* (sensu stricto) to include only northern specimens.

***Litoria majikthise* sp. nov.**
(Figs 1-4)

MATERIAL EXAMINED

HOLOTYPE: SAMR44093, 6km SSW Tabubil, Western Province, Papua New Guinea, 5°18'S, 141°12'E, G.R. Johnston, S.J. Richards, 10.vii.1993, male.

PARATYPES: UPNG6734, Megalsimbip, Ok Menga, Western Province, Papua New Guinea, 5°18'S, 141°20'E, J.C. Pemetta, vii.1981; UPNG7305-7309, Lower Kam valley, Western Province, Papua New Guinea, 5°12'S, 141°14'E, J. Menzies, i.1985; UPNG8501-8508, 6km SSW Tabubil, Western Province, Papua New Guinea, 5°18'S, 141°12'E, S.J. Richards, G.R. Johnston, 28.xi.1991; SAMR44094, 11km SSW Tabubil, Western Province, Papua New Guinea, 5°21'S 141°12'E, G.R. Johnston, S.J. Richards, 22.vii.1993; SAMR44095-44101, 6km SSW Tabubil, Western Province, Papua New Guinea, 5°18'S 141°12'E, G.R. Johnston, S.J. Richards, 9-10.vii.1993; UPNG8602-03, 12km S Tabubil, Western Province, Papua New Guinea, 5°22'S 141°17'E, G.R. Johnston, S.J. Richards, 1-20.vii.1993.

DIAGNOSIS

A member of the *Litoria nigropunctata* species group (Menzies 1972, 1993). Distinguishable from all other members of this group by the following combination of characters: 1, green dorsally in life; 2, snout-vent length 30.5-35.4mm in adult males; 3, thighs and groin crimson in life; 4, purple speckling on lateral surfaces of belly tending to form patches which do not separate distinct large, white lateral patches from venter; 5, distinct white postocular spot; 6, call with dominant frequency of 2.5kHz, a pulse repetition rate of 0.16-0.24 pulses/ms.

DESCRIPTION

Body size small (SVL=30.5-35.4mm in males, 39.2mm in a female). Head slightly broader than long or as broad as long (HL/HW = 0.81-1.03).

TABLE 1. Measurements of adult male *Litoria iris*, *L. leucova* and *L. majikthise*. Values are means (standard deviations). The measurements are defined in the text. *P* = probabilities associated with oneway ANOVAs comparing the taxa.

| Character | <i>L. majikthise</i> (N=14) | <i>L. iris</i> (N=13) | <i>L. leucova</i> (N=5) | P |
|-----------|--------------------------------|--------------------------|----------------------------|-------|
| SVL | 32.7 (1.659) | 31.4 (3.111) | 26.1 (0.391) | 0.000 |
| HW | 9.8 (0.395) | 9.5 (0.647) | 8.8 (0.363) | 0.006 |
| HL | 8.9 (0.622) | 8.1 (0.806) | 7.6 (0.466) | 0.003 |
| ED | 4.0 (0.412) | 3.6 (0.456) | 3.0 (0.164) | 0.000 |
| EN | 3.0 (0.283) | 2.6 (0.166) | 2.3 (0.123) | 0.000 |
| IN | 3.6 (0.181) | 3.5 (0.420) | 2.7 (0.205) | 0.000 |
| TL | 18.4 (0.547) | 18.2 (1.719) | 14.2 (0.383) | 0.000 |

Head length about one quarter of body length (HL/SVL = 0.24–0.29). Snout prominent, round when viewed from above and slightly round to truncate in profile. Nostrils lateral. Eye-to-naris distance less than or equal to internarial span (EN/IN = 0.72–1.03). Nostrils much closer to end of snout than eye. Canthus rostralis rounded, concave and slightly to well defined. Eyes large and protuberant, eye diameter generally greater than distance from eye to nostril (ED/EN = 0.97–1.55). Tympanum covered with skin, one third to one half of eye diameter. Vomerine teeth on two slight elevations between the choanae. Tongue broad and oval in shape.

Fingers short with moderate lateral fringes; finger lengths 3>4>2>1. Terminal discs large. Webbing to subarticular tubercle at base of penultimate phalanx of fourth finger. Hindlimbs moderately long (TL/SVL = 0.53–0.60); toe lengths 4>3>5>2>1. Webbing between toes to base of disc on all toes, except fourth and fifth. Webbing on fourth toe to base of penultimate phalanx. Webbing on fifth toe reaches midway along penultimate phalanx, continuing to disc via a narrow fringe. A small, oval inner metatarsal tubercle present; no outer metatarsal tubercle.

Skin of dorsal surfaces minutely tubercular. Throat and chest slightly granular. Few tubercles on posterior surface of forearm and outer edge of each foot. Few conspicuous tubercles on ventromedial surfaces of thighs, below anus. Posterior surface of thighs generally smooth, but interrupted by few large tubercles. Supratympanic fold inconspicuous.

In preservative dorsal surfaces immaculate blue (one specimen) or densely mottled with darker blue (all other specimens). Ventral surfaces generally cream to white, but ventral sur-

faces of hindlimbs, concealed parts of thighs, groin and in some specimens much of the belly pale pink. Lateral surfaces of throat and body with blue-grey stippling, sometimes developing into large dark patches in the groin and on throat. Some stippling may also occur on the posterior surface of thighs. A distinct, broad white postocular bar between eye and forelimb, running below the tympanum.

In life dorsal surfaces immaculate dark green or pale emerald green with darker green mottling. Ventral surfaces generally white; ventral surfaces of hindlimbs and belly red. Lateral surfaces of throat and body speckled with purple, sometimes developing into large dark purple patches in the groin and on throat. Stippling also present on posterior surface of thighs in some specimens. A distinct broad, pearl-white postocular bar, between eye and forearm, below tympana. Iris golden yellow.

Measurements of holotype (in mm). SVL = 34.0; HL = 9.0; HW = 10.8; ED = 4.5; EN = 3.1; IN = 3.9; TL = 18.7; FL = 23.1.

MATING CALL

Two types of call are uttered (Fig. 4B,D). One is a short (26–80ms, mean = 40, SD = 18.06, N = 7), harsh 'chip' consisting of 6–16 pulses (mean = 8.9, SD = 3.29) at a pulse rate of 0.20–0.24 pulses/ms (mean = 0.22, SD = 0.013). This short call begins at 2.2–3.2kHz and finishes at 1.4–4.3kHz, but has a dominant frequency around 2.5kHz. The second longer (290–360ms, mean = 330, SD = 36.1, N = 3) call is a harsh 'raagh', increasing in volume, consisting of 49–63 pulses (mean = 57.3, SD = 7.37) at a rate of 0.16–0.19 pulses/ms (mean = 0.174, SD = 0.010). This long call begins at 1.8–2.2kHz and ends at 1.8–5.0kHz, but has a dominant frequency around 2.5kHz. A number of individual frogs were heard to utter both short and long calls (including the holotype). Twenty calls uttered by four individuals gave a mean call rate of one per 26s. All calls were recorded at temperatures of 21.0 to 22.2°C.

ETYMOLOGY

From 'Majikthise' a farcical comedy character (Adams, 1979), referring to the vividly coloured thighs and groin.

DISTRIBUTION AND HABITAT

Known only from altitudes between 550 and 650m in the headwaters of the south draining Ok Tedi in the Star Mountains. Specimens were collected at night on foliage at the edge of cultivated



FIG. 2. A, B, *Litoria majikahise*; C, *Litoria leucova*. A, C, lateral views; B, ventral view.

sago swamps, among grasses in uncultivated swamps and on vegetation along a roadside ditch, all within 15km of the township of Tabubil. Perch heights varied between 1.0m and 2.5m.

Litoria leucova (Tyler, 1968)
(Figs 1-4)

Hyla leucova Tyler, 1968: 119.

MATERIAL EXAMINED

HOLOTYPE: SAMR6461, Busilmin, Sandaun Province, Papua New Guinea, 4°55'S 141°00'E, B. Craig, 1.v.1965, female.

OTHER MATERIAL: SAMR44091-44092, UPNG8604-06, Stolle Mountain, Sandaun Province, Papua New Guinea, 4°48'S 141°39'E, G.R. Johnston, S.J. Richards, 4.vii.1993.

DIAGNOSIS

Distinguishable from all other Papua New Guinean *Litoria* by the following combination of characters: 1, Green dorsally in life; 2, Snout-vent length 30.5-35.4mm in adult males; 3, thighs and groin translucent pink with yellow spots in life; 4, no purple speckling on lateral surfaces of belly; 5, no white postocular spot; 6, calls with dominant frequency of 4.0-5.0kHz, a pulse repetition rate of 0.11 pulses/ms.

DESCRIPTION

Body size small (SVL=30.5-35.4mm in males, 30.4mm in a female). Head slightly longer than broad (HL/HW=0.81-0.91). Head length about one third of body length (HL/SVL=0.26-0.31). Snout not prominent, round when viewed from above and truncate in profile. Nostrils lateral. Eye-to-naris distance less than internarial span (EN/IN=0.78-0.96). Nostrils closer to end of snout than to eye. Canthus rostralis straight and slightly defined. Eyes moderate in size, not prominent. Eye diameter fractionally greater than distance from eye to nostril (ED/EN=1.25-1.43). Tympanum visible, one half of eye diameter. Vomerine teeth absent. Tongue oval in shape with strongly indented posterior border.

Fingers short with broad lateral fringes; finger lengths 3>4>2>1. Terminal discs large. Webbing to subarticular tubercle at base of penultimate phalanx of fourth finger. Hindlimbs long and slender (TL/SVL=0.53-0.55); toe lengths 4>5>3>2>1. Webbing between toes to base of disc on all toes, except fourth. Webbing on fourth reaches halfway up penultimate phalanx and connected to disc by broad lateral fringe. Small, oval inner metatarsal tubercle present; no outer metatarsal tubercle.

Skin of dorsal surfaces smooth, except for weakly tubercular upper eyelids. Throat smooth. Chest and anterior portion of abdomen, and ventral surfaces of thighs granular. Large prominent tubercles on ventromedial surfaces of thighs, below anus. Supratympanic fold prominent, extending from posterior corner of eye, covering upper rim of tympanic annulus.

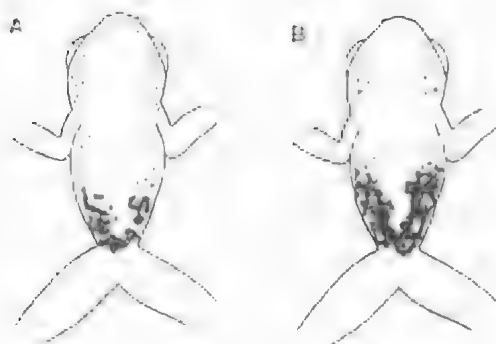


FIG. 3. A, *Litoria majikthise*; B, *L. iris*. Ventral view showing that the purple (black) of *L. majikthise* does not separate distinct white lateral patches from the remainder of the venter as it does in *L. iris*.

In preservative dorsal surfaces immaculate dark blue. Ventral surfaces white. Hidden surfaces of the thighs stippled with dark blue; this stippling is absent from numerous small circular areas so that ground colour appears in the form of circular spots. Subanal tubercles creamish white.

In life dorsal surfaces pale emerald green with occasional paler green spots on some individuals. Ventral surfaces generally white. Thighs and anterior lateral surfaces translucent pink with yellow spots. Iris golden yellow.

MATING CALL

Two types of call were uttered (Fig. 4A,C). One is a short (15-20ms, $N=23$), harsh 'chip' consisting of a single pulse. This short call begins at 3.5-6.0kHz for 10-15ms, then broadens to 2.0-6.0kHz for the last 5ms. The dominant frequency was 4-5kHz. The second longer (90ms, $N=1$) call is a harsh 'raagh', consisting of 10 pulses at a rate of 0.11 pulses/ms. This call began with three pulses between 4.0 and 5.5kHz, followed by nine pulses between 2.0 and 5.5kHz. The dominant frequency was 4.0-5.0kHz for the first nine pulses and then shifted to 2.0-3.0kHz for the last pulse. Two individuals were heard to utter both short and long calls in long, series. Twenty four calls by a single frog gave a mean call rate of one per 2.6s for short calls and one call per 60 s for long calls. Calls were recorded at a temperature of 17.6 C.

DISTRIBUTION AND HABITAT

Known only from two localities on the northern slopes of the central mountains. Specimens were collected while they called from piles of sticks overhanging streams running into a recently

cleared swamp and from vegetation overhanging a swift-flowing stream at 1600m altitude.

COMPARISON OF *LITORIA LEUCOVA* WITH *L. MAJIKTHISE*

Litoria leucova is smaller and therefore differs in most absolute body measurements from *L. majikthise* (Table 1). The correlations between the measurements and the discriminant functions indicate that, apart from its smaller size, *L. leucova* has a longer head, more prominent snout and smaller eyes than *L. majikthise*. Vomerine teeth are absent in *L. leucova* but present in *L. majikthise*.

The two species also differ in colour (Fig. 2). In life the presence of crimson red in the groin and on the thighs in *L. majikthise* clearly differentiates it from *L. leucova*, in which the thighs are translucent pink with yellow spots. However, this difference is less clear in preserved specimens as the crimson colour of *L. majikthise* fades. The presence of purple stippling on the ventrolateral surfaces of the body clearly distinguish *L. majikthise* from *L. leucova*, in which the ventral surface is white. All but one specimen of *L. majikthise* was strongly mottled dorsally, whereas *L. leucova* is generally immaculate pale green dorsally with the occasional paler spot on some individuals. The only *L. majikthise* to lack dorsal mottling was dark green on the dorsum. A pearly white postocular spot is present in *L. majikthise*, but absent in *L. leucova*.

The calls of *L. leucova* have a higher dominant frequency (4-5kHz) than those of *L. majikthise* (2-3kHz). Both species utter distinct short and long calls. The short calls of *L. leucova* consist of a single pulse and are 15-20ms long, whereas the short calls of *L. majikthise* consists of 6-16 pulses and are 26-80ms long. A single long call of *L. leucova* consisted of 10 pulses and was 90ms long, whereas the long call of *L. majikthise* was longer (290-360ms) and contained more pulses (49-63). *L. leucova* calls at a much faster rate (1 call/2.6s) than does *L. majikthise* (1 call/26s), so that it is difficult to know whether the series of short and long calls uttered by *L. leucova* is a series of separate mating calls or a single call consisting of these subunits.

Litoria leucova occurs at much higher altitudes (1600m) than does *L. majikthise* (550-650m). They may also differ in habitat preferences; *L. majikthise* was found in swamps or along a small, slow-flowing creek, whereas *L. leucova* was found calling from streams flowing through a

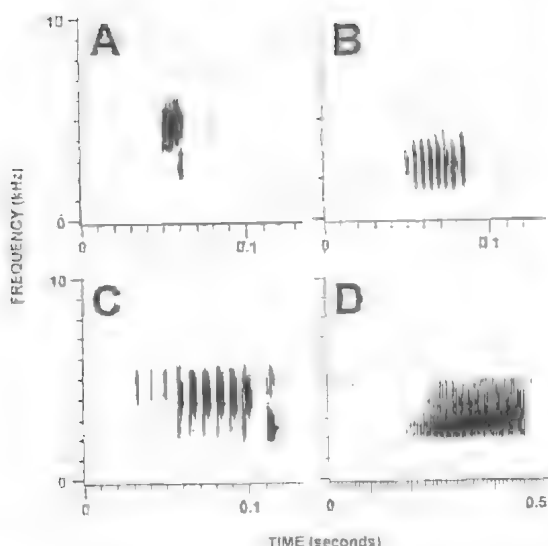


FIG. 4. Sonograms of calls. A,C, *Litoria leucova*; B,D, *L. majikthise*, holotype. Upper: short call. Lower: long call. Note that the scales on the abscissae differ between panel D and all other panels.

cleared area that had until recently been a swamp and along a well vegetated, swiftly flowing stream.

COMPARISON OF *LITORIA MAJIKTHISIE* WITH OTHER SPECIES OF *LITORIA*

Litoria majikthise has purple ventrolateral patches in common with *L. iris* and *L. ollauro* (Menzies, 1993), and which distinguishes these three species from all other species of *Litoria*. The purple patches of *L. majikthise* are smaller than those in *L. iris*, and do not separate distinct large, white lateral patches from the venter as in *L. iris* (Fig. 3). *L. majikthise* has crimson in the groin and on the thighs, whereas *L. iris* has yellow to orange and *L. ollauro* has orange (Tyler, 1962; Menzies, 1993).

In the Ok Tedi area *L. iris* occur within 20 kilometres of *L. majikthise* (Hyndman & Menzies, 1990), but *L. iris* is a montane species and occurs at much higher altitudes (1300–2300m; Tyler, 1968) than does *L. majikthise*.

Comparison of the call of *L. majikthise* with that of *L. iris* (based on Menzies, 1972, 1993) show no differences in the fundamental frequency, but the pulse rate is lower in *L. iris* (0.09–0.10 pulses/ms) than in *L. majikthise* (0.16–0.24 pulses/ms). Menzies (1975) described the call of *L. iris* as a slow buzzing or spluttering which is

clearly distinguishable from the harsh 'chip' or a harsh 'raagh' of *L. majikthise* (Menzies, 1993; pers. obs.).

COMPARISON OF *LITORIA LEUCOVA* WITH OTHER SPECIES OF *LITORIA*

Tyler & Davies (1978) placed *L. leucova* in a monotypic species group, defined by being small, uniformly green, montane frogs, with short, half-webbed fingers, fully webbed toes and unpigmented eggs. Tyler (1968) noted that the granules on the ventral surface of the holotype of *L. leucova* tend to form transverse ridges. Examination of the type and live specimens suggest that this characteristic is an artefact of preservation and not a structural feature of the frogs themselves.

The only other species of similar size to *L. leucova* which lay unpigmented eggs include some members of the *L. nigropunctata* group and all members of the *L. becki* group (sensu Tyler & Davies, 1978). Species in the *L. becki* group differ from *L. leucova* in having long unwebbed (vs short 1/3 webbed) fingers and a ventral surface variegated with dark pigments (vs white). *L. leucova* is similar to members of the *L. becki* group in that it has been found along a swiftly flowing mountain stream, but some *L. leucova* were collected from small streams which flowed through what had recently been a swamp. Thus the true habitat preferences of *L. leucova* are difficult to assess.

Of the species belonging to the *L. nigropunctata* group, *L. leucova* differs from *L. havina* Menzies, 1993, *L. mucro* Menzies, 1993 and *L. pronimia* Menzies, 1993 in that males lack a rostral spike (Menzies, 1993). *L. vocivincens* Menzies, 1972 occurs only on the southern lowlands of New Guinea and the hidden surfaces of the thighs are black (vs pink) (Menzies, 1972). *L. ollauro* and *L. iris* have large purple ventral patches, which *L. leucova* lacks (Tyler, 1962; Menzies, 1993). Dorsally *L. nigropunctata* (Meyer, 1874) is usually brown or green-brown (vs pale green) and the hidden surfaces of the thighs of are black (vs pink) (Menzies, 1972). *Litoria chloronata* (Boulenger, 1911) is the species which most closely resembles *L. leucova* in the *L. nigropunctata* groups, but its call has a lower dominant frequency (2.6kHz) than *L. leucova* and the concealed surfaces of the thighs and groin are bright orange (Menzies, 1993). The only species in the *L. nigropunctata* group that occur at altitudes higher than 1000m is *L. iris*.

Litoria leucova differs from most congeners in lacking vomerine teeth. *Litoria chloronata* and some *L. iris* share the lack of vomerine teeth with *L. leucova* (Tyler, 1962, 1968) as do members of the *L. bicolor* species group (Tyler & Davies, 1978). *Litoria leucova* differs from all members of the *L. bicolor* group in being of more robust habitus, and having unpigmented eggs.

Litoria leucova shares features in common with members of both the *L. becki* and the *L. nigropunctata* species groups of Tyler & Davies (1978). Unfortunately, neither of these groups can be defined by a single synapomorphy, and are almost certainly not monophyletic. Indeed, there is little correspondence between hypothesised relationships among species of *Litoria* based on morphological (Tyler & Davies, 1978), karyotypic (King, 1981) and immunological data (Hutchinson & Maxson, 1987). We have tentatively referred *L. majikthise* to the *L. nigropunctata* group because of its obvious similarity to *L. iris*, a species which has long been included in this group (Menzies, 1972, 1993). The affinities of *L. leucova* are less clear and will only be resolved by a thorough phylogenetic analysis of this speciose genus based upon all available data.

COMPARATIVE MATERIAL EXAMINED

Litoria iris: UPNG4434, 4478-79, Moiyakabip, Hindenberg Range; UPNG2318, UPNG7313-7318 Bakonabip; UPNG2101, Margariau; UPNG2117-2158, 2241-2281, Nipa; UPNG3115-3135, Tari; UPNG3150-3178, Komo; UPNG3674, 5528, Mendi; UPNG3844, Tambul; UPNG8289-90, Ubaigubi Lodge; UPNG6992-3, 7168, 7655, Mt Gilwe; UPNG5812-13, 5898-5903, Halalinja via Nipa; UPNG7023-7024, Angalimpeamp; UPNG7148-7167, Porgera; SAM5241, Okapa; SAM5423, 5874, Telefomin; SAM5726, Dumun.

ACKNOWLEDGEMENTS

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lyse calls. Our work in New Guinea could not have been done without the help of Roselyn Busasa (Institute of Papua New Guinea Studies), Dr Navu Kwapena (Department of Environment and Conservation, PNG), and Drs James Menzies and Ian Burrows (University of Papua New Guinea). Dr Margaret Davies and Mike Tyler commented on the manuscript.

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THE HASTINGS RIVER MOUSE, *PSEUDOMYS ORALIS*, FROM GAMBUBAL STATE FOREST, SOUTHEAST QUEENSLAND. *Memoirs of the Queensland Museum* 17(1): 280-1994. *Pseudomys oralis* is a poorly known, perhaps rare, Australian species of murid rodent. The few recorded localities at which live specimens have been captured are all in eastern New South Wales and southeastern Queensland (Ingram & Raven, 1991). Skeletal remains found in "geologically recent cave deposits" in the Great Dividing Range in Victoria and New South Wales, and in "relatively fresh owl pellets" near Maleny, Queensland (Kirkpatrick, 1983: 394), suggest that the Hastings River Mouse once had a much wider distribution (Watts & Aslin, 1981). Three *P. oralis* captured at Gambubal State Forest (SF) (Queensland SF Forest (66): 28°30'S, 152°27'E) between April and July 1993 are the first records of this species from Queensland in more than 20 years.

Gambubal SF is situated on the western slopes of the Great Dividing Range near Warwick, between altitudes of 1080m and 1196m. Vegetation types in the area include complex myrtophyll vine forest, tall open eucalypt forest, open tussock grassland with interspersed herbs and ecotonal communities. The vine forest was logged in the 1950's and early 1960's (Dale, 1983) and the tussock grassland and eucalypt forest have been disturbed by varying intensities of fire and cattle grazing. Mean annual rainfall is 1199mm over the last 36 years, and mean monthly temperatures range from 25.2°C in January to 4.9°C in July. Rainfall is expected to be higher and the range of temperatures greater, at the higher elevations where *P. oralis* was captured.

The captures of small mammals reported here were made in the course of routine transect trapping, initiated in April 1993, to investigate the vine forest grassland and the vine forest eucalypt forest ecotones. At each ecotone two parallel trap lines, 200m long and 100m apart, were established across the habitat interfaces. Each line included 20 trapping stations. Two type A Elliott traps (30 x 10 x 9cm) baited with sweet potato soaked in vegetable oil and bacon were used at each station.

P. oralis were captured only on the vine forest eucalypt forest transect lines. On April 24, 1993 one adult female (76g) with enlarged, recently post-lactation teats was captured in open eucalypt forest 75m from the vine forest edge. The animal was ear-tagged and released. On April 25, 1993 it was recaptured on the same transect line 65m from the vine forest edge. On the same day a second adult female (86g) was captured on the other transect line, 95m from the vine forest edge. An immature male *P. oralis* (70g) was captured on June 22, 1993; it was taken on the first transect line, 5m within the vine forest. This individual was recaptured at the same station on July 23, 1993 (77g). At this time it had fully descended testes.

The five captures of three *P. oralis* have been obtained in the course of 720 trap nights; 360 within open eucalypt forest and 360 within vine forest. Additional captures have been 9 *Rattus fuscipes*, 18 *Rattus lateralis*, 1 *Melomys cervinipes*, 32 *Antechinus stuartii* and 3 *Sminthopsis murina* in the open eucalypt forest and 39 *Rattus fuscipes*, 11 *Melomys cervinipes* and 53 *Antechinus stuartii* in contiguous vine forest on the same transect lines.

At Gambubal SF the open eucalypt forest is dominated by New England Blackbutt (*Eucalyptus campanulata*) with a dense ground cover of blade grass (*Imperata cylindrica*), some kangaroo grass (*Themeda triandra*) and snow grass (*Poa labillardieri*), bracken (*Pteridium esculentum*) and herbs. Burnt logs are abundant but little leaf litter is evident. The area in which the traps were located was unburnt for about 20 years before a mild fire in November 1990. Between 100 and 150m from the edge of the vine forest, the land slopes steeply down to the Condamine gorge. *Acacia* saplings growing along the slope indicate that fire intensity may have been greater here

than at the higher altitude where *P. oralis* were captured. The area is relatively inaccessible to stock; it was free of cattle grazing until 1991 and grazing disturbance appears to be minimal. The transition from open eucalypt forest to vine forest is abrupt and the site where the male *P. oralis* was captured is unlike locations within the eucalypt forest; grass was absent from the understorey and there was a thick layer of leaf litter beneath a moderately dense canopy of typical vine forest shrubs and vines, dominated by *Eucalyptus dumalis*.

Kirkpatrick (1983: 394) reported that captures of *P. oralis* were made "alongside fallen logs lying near low creek banks in tall, open eucalypt forest with substantial growth of bracken". He recorded adult weights of 90-100g. Earlier captures from Queensland by Kirkpatrick & Martin (1971: 114) were made in a bracken fern-covered creek bank in open eucalypt forest, about 20 miles from Warwick in the foothills of the Great Dividing Range (Covacevich & Easton, 1974: 32; Hyatt & Shaw, 1980). These captures were obtained at 600m altitude, approximately 10 km SW from Gambubal State Forest. The captures reported from Gambubal State Forest are from a substantially higher altitude (i.e. 1100m) and are distant from watercourses, indicating that the sites at which *P. oralis* has been previously caught may not be wholly representative of their habitat. The recent breeding status of the two females taken in April suggests that the animals were not transient within the area that was trapped. In August 1993, subsequent captures of *P. oralis* were obtained at this site by the Department of Environment and Heritage, and a male specimen (84g) collected on August 14, 1993, is lodged at the Queensland Museum (QMJM9994).

Observations reported in this paper confirm the continued survival of *P. oralis* in southeastern Queensland and extend the range of environments in which the species may be found.

Acknowledgements

I would like to thank the Department of Environment and Heritage for permission to trap and the Department of Botany, University of Queensland for facilitating access to their research sites. I am also grateful to Steve Phillips for discussion and encouragement, to Peter Dwyer for confirming identification of the animals, and to Yvonne Ross, from the Department of Botany, University of Queensland, for providing the habitat description.

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A REMARKABLE NEW ASTEROPHRYINE MICROHYLID FROG FROM THE MOUNTAINS OF NEW GUINEA

STEPHEN J. RICHARDS, GREGORY R. JOHNSTON AND THOMAS C. BURTON

Richards, S.J., Johnston, G.R. & Burton, T.C. 1994 12 01: A remarkable new asterophryine microhylid frog from the mountains of New Guinea. *Memoriae of the Queensland Museum* 37 (1): 281-286. Brisbane. ISSN 0079-8835.

Asterophrys leucopus sp. nov. is described from mid-montane rainforest on the slopes of Stolle Mountain in central New Guinea. It is the second known species of this genus, hitherto containing only the poorly known and morphologically bizarre *A. turpicula*. *Asterophrys leucopus* shares with *turpicula* an extremely broad head (almost 50% of SVL), and a skull with a distinct sagittal crest, but lacks elongated, conical spines on the eyelids, prominent subarticular tubercles of the hands and feet, and has a different mating call. □ *Frog, new species, Asterophrys leucopus, Microhylidae, Asterophryinae, New Guinea.*

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Microhylid frogs are a speciose group that exhibit considerable ecological and morphological diversity in the rainforests of New Guinea (Zweifel, 1972). Two subfamilies, Genyophryinae and Asterophryinae, are recognised in the Australopapuan region, but the Asterophryinae are confined to New Guinea and its satellite islands (Zweifel, 1972). In a recent revision of this subfamily Burton (1986) recognised 43 species in 8 genera, three of which (*Asterophrys*, *Hylophorbus*, *Pherohapsis*) were monotypic.

Zweifel (1972) defined *Asterophrys* as possessing fused and rugose nasals, a high, thin sagittal crest on the frontoparietals, and heavy, rugose squamosals which in some specimens join broadly to the maxillae anteriorly. Burton (1986) combined a number of genera (*Asterophrys*, *Hylophorbus*, *Mantophryne*, *Pherohapsis*) in the tribe Asterophryini, characterised by a highly crested ilium, absence of muscle fibres from the dorsal surface of the frontoparietals, reduction of the m. geniohyoideus lateralis internus, a distal origin of the m. tibialis anticus brevis and large subarticular tubercles. *Asterophrys* as conceived by Burton (1986) differs from the rest of the tribe in possessing two supplementary slips to the m. intermandibularis, division of the m. adductor mandibularis posterior longus into two segments, warts on chin large, and the diagnostic characters described by Zweifel (1972). The discovery of a second species of *Asterophrys* allows a refinement of the diagnosis of the genus.

Morphologically, *Asterophrys turpicula* is one of New Guinea's most distinctive frogs. It is a

large microhylid (to 65mm; Parker, 1934) with a broad head and elongated spines on the eyelids. Despite its large size and bizarre appearance, it is a poorly known species; biological information is limited to observations on the diet of several museum specimens (Brongersma, 1953) and the tantalising observations of F. Parker that this species 'calls like a kitten's miaow, and bites and attacks hands quite viciously' (Zweifel, 1972). Although known from widely scattered localities in the western half of the island of New Guinea, *A. turpicula* is represented by few specimens in museum collections (Menzies, 1985).

During surveys of the frog fauna of the mountains of central New Guinea SJR & GRJ made further observations on *A. turpicula* and collected a new species of *Asterophrys* from Stolle Mountain in the headwaters of the Sepik River. Here we describe the new species, and present observations on the biology, mating call and aggressive behaviour of *A. turpicula*.

The new species is a microhylid, confirmed by possession of the m. rectus abdominis pars anteroflecta (Burton, 1980), and an asterophryine, exhibiting the symphygnathous condition (Parker, 1934; Zweifel, 1972). The crested ilium is typical of the tribe Asterophryini, as is the exclusion of muscle fibres from the dorsum of the frontoparietals. This species exhibits the characters unique to *Asterophrys* within the tribe e.g. possession of two supplementary slips to the m. intermandibularis, but the warts on the chin are smaller than those of *A. turpicula*. All of the diagnostic characters of Zweifel (1972)



FIG. 1. *Asterophrys leucopus* sp. nov., Stolle Mountain, Sandaun Province, Papua New Guinea.

are present: the nasals are fused and rugose; the frontoparietals are compressed into a high sagittal crest, the ridge of which is rugose; and the squamosal is enlarged and rugose, broadly contacting the maxilla anteriorly. The only respect in which this species does not conform to the definitions is the poor development of its subarticular tubercles. Given that this is clearly an *Asterophrys* by all other criteria, Burton's (1986) definition of the tribe Asterophryini must be revised to 'subarticular tubercles usually large and prominent'.

Methods of measurement (in millimetres) follow Zweifel (1972). SVL=snout-vent; TL=tibia length; EN=eye-naris; IN=internarial distance; SN=snout-naris distance; HW=head width; HL=head length; ED=eye diameter. Measurements of ear diameter are excluded because the tympanum of this species is indistinct. Minimal dissection was performed to give access to the musculature and bones of the skull, and superficial musculature of the throat and abdomen relevant to the generic diagnosis. Deep features such as the m. geniohyoideus and m. tibialis anticus brevis were not examined. We have not examined types of the two species synonymised

with *Asterophrys turpicula*; *A. leopoldi* and *A. steini*. The status of these species was addressed by both Brongersma (1953) and Zweifel (1972).

Specimens are deposited in the following museums; Queensland Museum (QM), University of Papua New Guinea (UP) and South Australian Museum (SAM).

SYSTEMATICS

Asterophrys leucopus sp. nov. (Figs 1-3)

MATERIAL EXAMINED

HOLOTYPE: QMJ58650, adult male, collected by S.J. Richards and G.R. Johnston, Stolle Mountain, Sandaun (West Sepik) Province, Papua New Guinea, 4°48'S, 141°39'E, 1600m, 4-5.vii.93.

PARATYPES: UP8442, SAMR43785, adult males, same collection data as holotype.

DIAGNOSIS

A moderately large microhylid frog, males 43.0-46.8 SVL, distinguished from all other Australopapuan microhylid frogs by the following combination of characters: head extremely broad (44.5-48.8% of SVL), frontoparietals com-

pressed into high sagittal crest, distinct tubercles on eyelids, palmar and plantar surfaces of hands and feet with greatly reduced pigmentation and poorly developed subarticular tubercles, six pale tubercles around lower jaw, mating call a musical series of rapidly repeated introductory notes and more slowly repeated terminal notes, uttered at irregular intervals.

DESCRIPTION OF HOLOTYPE

An adult male with the following measurements: SVL 43.0; TL 17.1; EN 4.3; IN 3.5; HW 21.0; HL 14.0; ED 5.0; SN 1.5; disc of third finger 1.2 (penultimate phalange 0.9); disc of fourth toe 1.2 (0.8). Body robust, limbs short (TL:SVL 0.39). Head almost triangular in dorsal view, snout steep, projecting beyond lower jaw, obtusely angular in lateral view; canthus rostralis straight, moderately defined (disrupted by tubercles); loreal region steep, slightly concave; nostrils lateral, much closer to tip of snout than to eye (EN/SN 2.9), eye to naris distance greater than internarial distance (EN/IN 1.2). A series of six distinct tubercles on the lower jaw (Fig. 2). Eyes small, orbit not visible in ventral view, pupil horizontal; tympanum indistinct. Vomerine teeth absent, vocal slits present, anterior palatal ridge short, posterior palatal ridge long, distinct, with 7 denticles. Relative lengths of fingers $3 > 4 > 2 > 1$; discs weakly developed, without grooves, but distinctly broader than penultimate phalanges, subarticular tubercles low and indistinct, no

metacarpal tubercles. Toes unwebbed, relative lengths $4 > 3 > 5 > 2 > 1$; discs weakly developed, same size as finger discs; subarticular elevations and inner metatarsal tubercle low and indistinct. Skin covered with scattered tubercles dorsally, tending to form longitudinal rows (Fig. 1); tubercles on eyelids large, prominent but not forming elongated conical spines (Figs 1, 2); skin almost smooth ventrally.

In preservative dorsum grey with irregular pinkish markings, sometimes bordered by black and concentrated as follows: on tubercles, some bordered by black and in others pinkish markings joined to form stripes along rows of tubercles. A wide pink longitudinal bar posteriorly on dorsum, bordered laterally by distinct black markings. No vertebral stripe. Ventral surface dark grey (almost black) anteriorly with pale flecks, becoming paler posteriorly with spots and mottling of pale cream. Palmar surfaces of hands almost completely white, pigmentation on plantar surfaces of feet reduced, restricted primarily to centre of plantar surface, absent on toes. Tubercles on lower jaw pale, tongue white.

VARIATION

The two paratypes are adult males. Selected measurements of these two specimens are (SAMR43785/UP8442): SVL 46.8/43.1; TL 17.4/16.6; EN 4.4/4.0; IN 2.1/3.3; HW 21.9/19.2; ED 4.8/5.4; SN 1.7/1.5. The main variation is in the colour pattern. In life all three specimens in

the type series are mottled light and dark pinkish brown, with irregular black patches on the dorsal and lateral surfaces. The tips of the dorsal tubercles are pink, and the prominent tubercles on the lower jaw, and palmar and plantar surfaces of the hands and feet, are pale cream. However one paratype (SAMR43785) has a pale cream vertebral stripe running the full length of the body. This stripe is thinner anteriorly, broadens to about 1.5mm posteriorly and continues along the entire length of each thigh.



FIG. 2. Head of *A. leucopus* sp. nov. showing distinct pale tubercles on jaw.

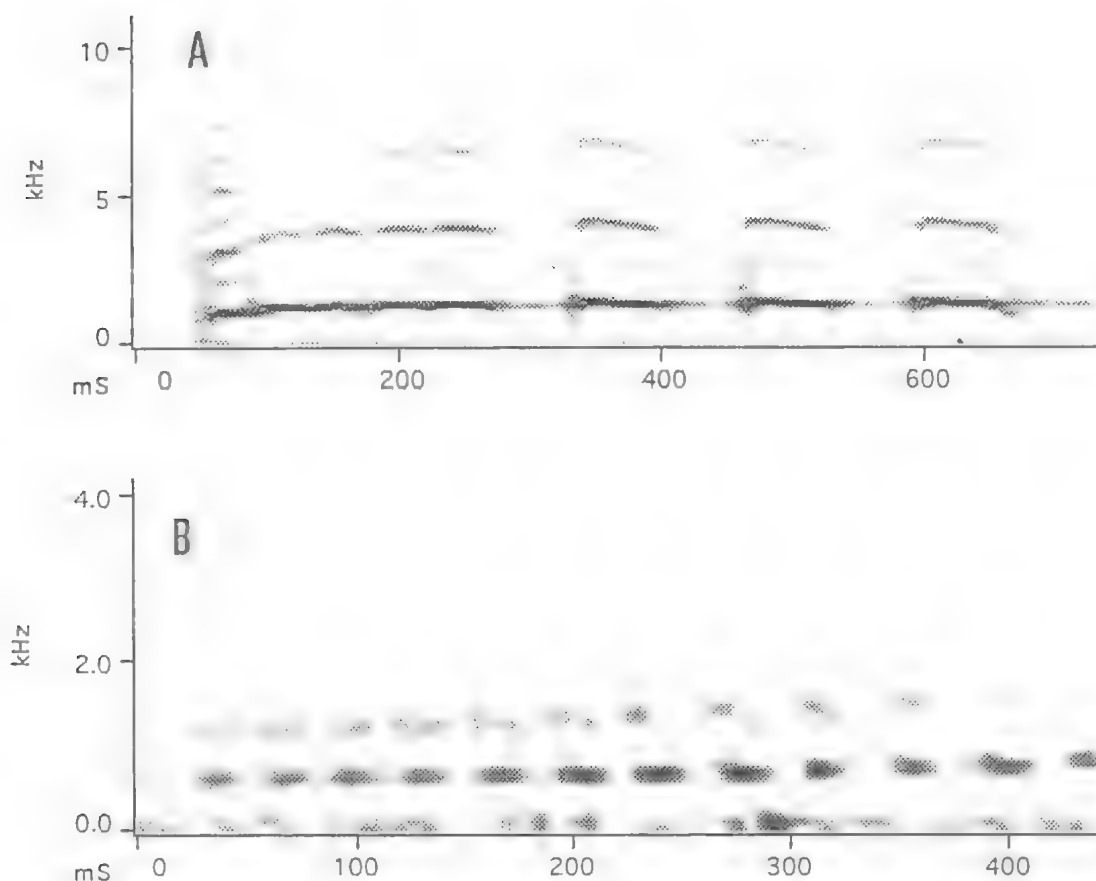


FIG. 3. Mating calls. A, *Asterophrys leucopus* sp. nov., holotype, QMJ58650, Stolle Mountain, Sandaun Province. Air temperature = 17.8°C; B, *A. turpicula*, near Kiunga, Western Province. Air temperature = 27.0°C.

MATING CALL

The call of *A. leucopus* is a series of rapidly repeated introductory notes followed by a series of slower terminal notes. A call recorded on 5.vii.93 (air temp. at calling site 17.8°C) lasted approximately 0.6s (Fig. 3A). The call is well tuned, the dominant frequency is about 1.25KHz, and the second and fourth harmonics are emphasised giving the call a musical quality. It is quite distinct from the call of *A. turpicula*, which is a short, ascending trill. A single call of *A. turpicula* recorded at Drimdemasuk Village, approximately 12km upstream from Kiunga on 14.xi.91 is illustrated for comparison in Fig 3B. The dominant frequency starts at 0.6 KHz and finishes at 0.8KHz. A distinct harmonic starts at 1.2KHz and finishes at 1.6KHz. The call lasts for 0.45s.

HABITAT AND HABITS

The holotype was calling from an exposed mossy tree root in closed canopy mid-montane rainforest at approximately 1600m on the slopes of Stolle Mountain. The two paratypes were collected from a mossy tree stump and the forest floor respectively. At this altitude most of the forest is covered with a thick layer of wet moss, against which the frogs were well camouflaged (Fig. 1).

The stomach of the holotype contained two large centipedes and a clump of moss, and one of the paratypes (SAMR43785) contained a small, partly digested microhylid frog (probably a *Cophixalus*) measuring 17.7 SVL.

Despite repeated handling we did not observe aggressive behaviour in *Asterophrys leucopus*. *A. turpicula*, with which it shares a number of bizarre morphological characters, exhibits two

forms of aggressive behaviour: (1) an aggressive posture in which the body is inflated and the mouth is held wide open exposing the blue tongue (Fig. 4), a posture similar to that displayed by the blue-tongued lizard *Tiliqua scincoides* and (2) lunging behaviour, in which the frog leaps at potential predators mouth agape, actively biting the 'predator' and often maintaining a strong grip for over 3 minutes. The blue tongue of this species is conspicuous during aggressive encounters.

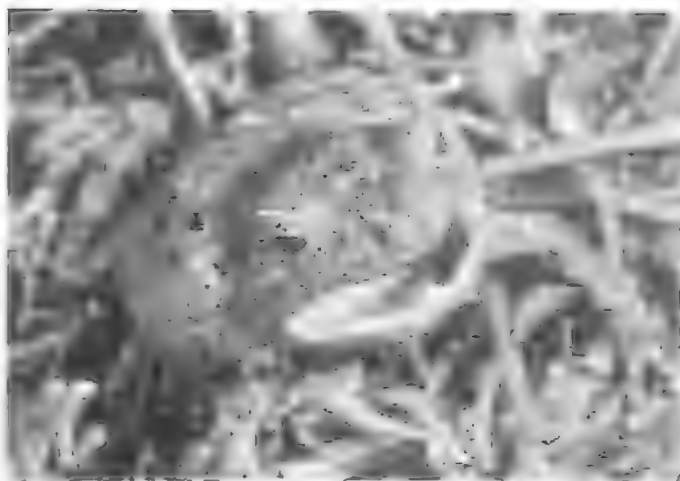


FIG. 4. Aggressive gaping behaviour of *Asterophrys turpicula* collected at Tabubil, Western Province, July 1993.

DISTRIBUTION

Known only from the type locality.

COMPARISON WITH OTHER SPECIES AND COMMENTS ON *A. TURPICULA*

Asterophrys leucopus is a morphologically distinctive microhylid frog, and only two species are likely to be confused with it. *Asterophrys turpicula* has a head as broad as *A. leucopus*, but differs in having the mid-dorsum smooth, in the possession of an elongated, spine-like tubercle on each eyelid, two prominent tubercles on the lower jaw that are the same colour as the dorsum, (vs 6 pale cream tubercles), a blue tongue, pigmented hands and feet, very distinct subarticular tubercles, and a different mating call (Fig. 3B). *A. turpicula* calls from below the surface of the forest floor, while *A. leucopus* calls from exposed positions.

The two species have not been found in sympatry. During our surveys *A. turpicula* was a common species in lowland and hill forest (to approximately 600m) between the Fly River (Kuambit, near Kiunga) and the southern foothills of the Star Mountains, Western Province, PNG. *A. turpicula* has adapted to disturbed environments and was common in suburban gardens in the mining town of Tabubil in November 1991 and July 1993; males were calling in both of these months suggesting that the breeding season is extended if not continuous in this perpetually wet environment (Hyndman &

Menzies, 1990). *A. leucopus* was not found at any sites between 60 and 3200m on the southern slopes of the Star Mountains. The type (and only known) locality for *A. leucopus* is on the northern side of the central cordillera, where all of the type series were collected in rainforest.

Genyophryne thomsoni is the only other microhylid with a head as broad as *A. leucopus*, but is a smaller species (maximum recorded SVL 38), lacks finger discs and the jaws are not symphygnathine (Zweifel, 1971; 1972).

ETYMOLOGY

From the Greek 'leukos' = white, 'pous' = foot, referring to the distinctive white (pale cream in life) feet of this species.

REMARKS

Through the courtesy of Mr James Menzies (UPNG) we have examined two *Asterophrys* specimens (UP8362 & UP8472) from the Vogelkop Peninsula of Irian Jaya. They are males, SVL 54 and 40 respectively and have enlarged and rugose squamosals and a sagittal crest. They differ from *A. leucopus* in having distinct subarticular tubercles and pigmented feet, and differ from both *A. leucopus* and *A. turpicula* in lacking large tubercles on the lower jaw. They further differ from *A. turpicula* in lacking blue colouration on the tongue in preservative. In most other respects they resemble *Asterophrys*, and it is likely that when additional

material is collected the generic definition of *Asterophrys* will have to be further refined.

ACKNOWLEDGEMENTS

Field work in Papua New Guinea by SJR & GRJ was funded in part by a grant from the Peter Rankin Trust Fund for Herpetology and a James Cook University Research Grant (to SJR). Ok Tedi Mining Limited provided invaluable logistical support in the field. We are particularly grateful to Murray Eagles, Ian Wood, Andrew Storey, Andy Mai and Kayemen Bakowa of the OTML Environment Department. The Gregory family, Rob Lachlan, James Menzies and Ian Burrows provided generous hospitality and assistance in PNG, and Keyt Fischer of Mekil Research Station enthusiastically supported our work on Stolle Mountain. Roselyn Busasa (Institute of Papua New Guinea Studies) and Dr Navu Kwapena (Department of Conservation and Environment) greatly facilitated the processing of our research visas and export permits respectively.

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SYSTEMATIC POSITION OF THE AUSTRALIAN FOSSIL OSTEOGLOSSID FISH
†*PHAREODUS* (= *PHAREOIDES*) *QUEENSLANDICUS* HILLS

LI GUO-QING

Li G.-q. 1994 12 01: Systematic position of the Australian fossil osteoglossid fish
† *Phareodus* (*Phareoides*) *queenslandicus* Hills. *Memoirs of the Queensland Museum* 37(1):
287-300, Brisbane. ISSN 0079-8835.

The Australian Tertiary teleost †*Phareoides* Taverne is a synonym of the fossil osteoglossid genus †*Phareodus*. Thus, †*Phareoides queenslandicus* is a junior synonym of †*Phareodus queenslandicus*. This Australian species of †*Phareodus* is phylogenetically most closely related to †*P. encaustus* from North America. The relationship is mainly supported by the frontal consisting of a narrow posterior portion and a greatly expanded anterior portion, the hyomandibular bearing a stick-like opercular process and a subtriangular anterior wing, the number of dentary teeth, the preopercle with an indistinct horizontal arm, and the pattern of the posterior infraorbitals. □ †*Phareoides*, †*Phareodus*, synonym, Australia, North America, Lower Tertiary.

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†*Phareodus queenslandicus* is a fossil osteoglossid named by Hills (1934) on the basis of materials from the Redbank Plains Formation of southern Queensland, Australia. It was considered to be similar either to the North American †*Phareodus acutus* [= †*Phareodus encaustus* (Cope) 1872, see Grande (1984) and this paper] in body shape and in the skull roof, or to the extant Australian *Scleropages leichardti* Günther, 1864 in the shape of the "post orbitals." Hills (1958) further believed that †*P. queenslandicus* might be the forebear of the Australian extant *Scleropages*. Roellig (1967) reached an opinion agreeing with Hills after his examining both fossil and extant osteoglossids. In contrast, Taverne (1973, 1974, 1978) asserted that †*P. queenslandicus* differs as much from the North American †*Phareodus* species as it does from †*Brychaetus* Woodward 1901; he thus coined another generic name, †*Phareoides* (see Taverne, 1973), for †*Phareodus queenslandicus*.

Recently, the Queensland Museum offered me an opportunity to reexamine specimens of †*Phareoides queenslandicus*. My examination yielded sufficient new information to allow a reassessment of the systematic position of this Australian fossil osteoglossid.

Specimens included in this study consist of fossils, dried skeletons of extant material, preserved, or cleared and stained extant specimens. All exclusively fossil taxa are marked with daggers (†) preceding their names throughout this paper.

MATERIALS

HIODONTIDAE: *Hiodon tergicus* Lesueur, specimens listed in Li & Wilson (in press), *Hiodon alosoides* (Rafinesque), specimens listed in Li & Wilson (1994), †*Hiodon consteniorum* Li & Wilson, specimens listed in Li & Wilson (1994). †*Eohiodon rosei* (Hussakof), UALVP12436 and specimens listed in Cavender (1966) and Wilson (1977). †*Eohiodon woodruffi* Wilson, specimens listed in Wilson (1978). †*Eohiodon falcatus* Grande, 14 specimens (FMNHPP9878-9880, 9882, 10424, 10633, 10634, 10639, 10955, 12516, 13063, 13064; ROM43220; and UALVP24203, SL ranging from 30 to 161mm). †*Yanbiania wangqingica* Li, specimens listed in Li (1987).

†LYCOPERIDAE: †*Lycopera davidi* (Sauvage), specimens including those listed in Liu et al. (1963), Ma (1987), and AMNHFF19400, 19403.

OSTEOGLOSSIDAE: *Osteoglossum bicirrosus* (Vandelli), one alizarin prepared specimen (UAMZ4642, SL = 177mm). *Osteoglossum ferreirai* Kanazawa, four alizarin prepared young specimens (UAMZ6753-6754, SL ranging from 48 to 61mm). †*Cretophareodus alberticus* Li, specimens listed in Li (in press). †*Phareodus testis* (Cope), 17 incomplete (AMNH743, 754, 805, 2467, 2471, and 8124; FMNHPP10241, 11939, 11941, 12412, 14061, 25439, and FMNHUF31; ROM28560, 29043 and 29076; UALVP12712) and 20 well-preserved (AMNH1336, 2799, 5821, 6301, 11547; FMNHPP10627, 10960, 10969, 11942, 11943, 12411, 12682, 13035, 13576, 25014, and

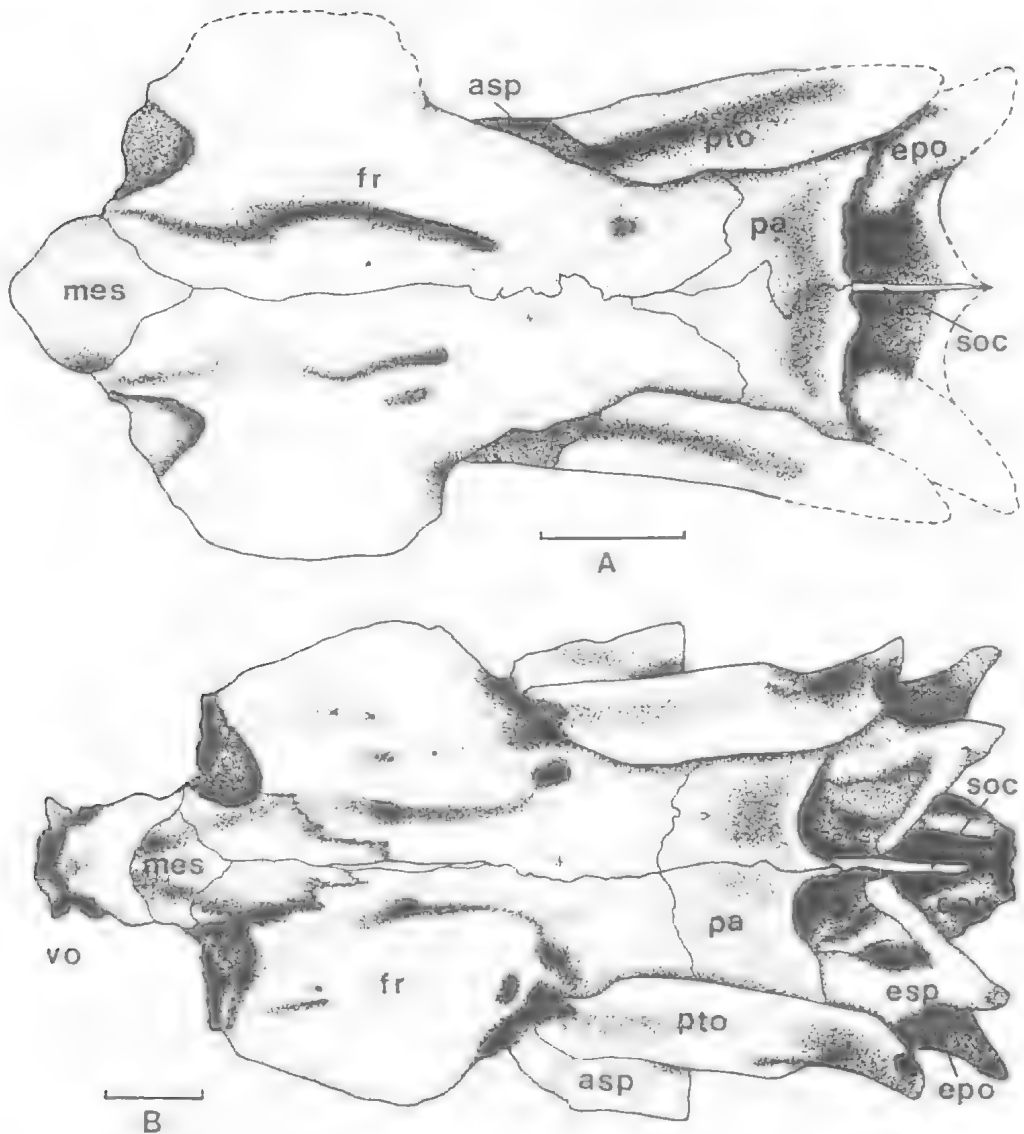


FIG. 1. Comparison of the skull roof between Australian and North American †*Phareodus* species. A, †*Phareodus queenslandicus*, QMF2917 (cast of UQF14960); B, †*Phareodus encaustus*, AMNH4587. Scale bars = 10mm. Note the "V-shaped" depression on the anterior margin area of each of the frontals, which receives the posterior end of the nasal in the two North American †*Phareodus* species as shown in Fig. 8 of this paper.

26407; UALVP447, 17657-17659. SL ranging from 39 to 304mm) specimens from the Green River Formation of Wyoming. †*Phareodus encaustus* (Cope). 16 incomplete (FMNHPF9891, 10255, 10257, 10963, 11938, 11952, 12515, 12683, 12685, 13103, 10961, 10962, 14064, and 14262; AMNH4587 and 8999) and 14 complete (FMNHPF10256, 10285, 10964-10967, 11944, 11954, 12408, 12409, 14040, 14062, 14063, 12681, SL ranging from 26 to 540mm)

specimens from the Green River Formation of Wyoming. †*Phareodus queenslandicus* Hills, casts of specimens listed in Hills (1934); *Arapaima gigas* (Cuvier), one specimen (UAMZ2244, SL=285mm). †*Sinoglossus lushanensis* Su, specimens listed in Su (1986).

PANTODONTIDAE: *Pantodon buchholzi* Peters, one alizarin prepared specimen (UAMZ6751,

SL=72mm) and three specimens preserved in alcohol (UAMZ2273, SL ranging from 60 to 67mm).

NOTOPTERIDAE: *Chitala chitala* (Hamilton) (see Roberts, 1992), four alizarin prepared specimens (UAMZ6756, SL ranging from 72 to 82mm). *Xenomystus nigri* (Günther), two complete alizarin prepared specimens (UAMZ2272, SL=132; UAMZ6752, SL=125mm).

METHODS

The extant fishes are either fixed in formalin and preserved in alcohol or cleared and stained with alizarin (e.g. UAMZ3969). Measurements and counts were made mainly following Hubbs & Lagler (1964). Terms used for description follow Nelson (1968, 1969, 1973), Kershaw (1976), Wilson (1977), Patterson & Rosen (1977), Grande (1984), Li (1987), Arratia (1987), Arratia & Schultze (1991), Grande & Cavender (1991), and Wilson & Williams (1991).

ABBREVIATIONS

Institutional. AMNH, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, USA; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; QM, Queensland Museum, Australia; ROM, Royal Ontario Museum, Toronto, Canada; UALVP, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Canada; UAMZ, Museum of Zoology, Department of Zoology, University of Alberta.

Anatomical. ang, angular; ao, antorbital; art, articular; asp, autosphenotic; boc, basioccipital; bpt, p, basipterygoid process on parasphenoid; br, branchiostegals; bs, basisphenoid; ch, anterior ceratohyal; clt, cleithrum; cm, coronomeckelian; den, dentary; d.hh, dorsal hypohyal; dsp, dermosphenotic; enp, endopterygoid; eoc, exoccipital; epo, epiotic; esp, extrascapular (supratemporal); fr, frontal; hm, hyomandibula; iol-5, 1st to 5th infraorbitals; mes, mesethmoid; mx, maxilla; na, nasal; op, opercle; os, orbitosphenoid; pa, parietal; pas, parasphenoid; pelt, postcleithrum; pmx, premaxilla; pop, preopercle; pt, posttemporal; pto, pterotic; pts, pterosphenoid; qu, quadrate; rart, retroarticular; sclt, supracleithrum; sm, symplectic; soc, supraoccipital; sop, subopercle; v.hh, ventral hypohyal; vo, vomer.

MEASURING AND MERISTICS

APR, principal anal fin rays; AP, anal pterygiophores; CFR, principal caudal fin rays; DFR, principal dorsal fin rays; DP, dorsal pterygiophores; H, hypurals; SL, standard length; TV, total vertebrae.

SYSTEMATIC PALAEOONTOLOGY

Subdivision TELEOSTEI Müller, 1846

Superorder OSTEOGLOSSOMORPHA

Greenwood et al., 1966

Order OSTEOGLOSSIFORMES Berg, 1940

Family OSTEOGLOSSIDAE Bonaparte, 1850

Subfamily OSTEOGLOSSINAE

INCLUDED GENERA

†*Cretophareodus* Li (in press), †*Phareodus*, †*Brychaetus*, †*Singida*, *Osteoglossum*, and *Scleropages*.

EMENDED DIAGNOSIS

Osteoglossids differing from Heterotinae in the following features: palatine fused with ectopterygoid; tooth plates on basihyal and first to third basibranchials fused with each other to form an elongate basibranchial dentition; first pectoral fin ray particularly strong and long, with its distal end extending to beyond pelvic fin; horizontal arm of preopercle short, ending anteriorly far behind orbit; opercle subsemicircular in shape; preoperculo-mandibular canal in an open groove on horizontal arm of preopercle.

REMARKS

The genera included in this subfamily may also be characterized by having a hyomandibular with a subtriangular anterior wing, mandibulo-quadrate articulation lying far behind orbit, posterior end of maxilla extending back to level of quadrate condyle.

†*Brychaetus* Woodward, 1901 is osteologically similar to both †*Phareodus* Leidy, 1873 and †*Phareoides* Taverner, 1973. A comparison of the observable preserved cranial skeleton of †*Phareoides queenslandicus* with that of †*Brychaetus muelleri* (see Roellig, 1974) and †*Phareodus encaustus* suggests possible synonymy of both †*Phareoides* and †*Brychaetus* with †*Phareodus* (see discussion below).

†*Singida* Greenwood & Patterson, 1967 is included in the subfamily Osteoglossinae in this paper because it shares at least the following characters with the extant *Osteoglossum* and *Scleropages*: 1) The postero-ventral edge of the

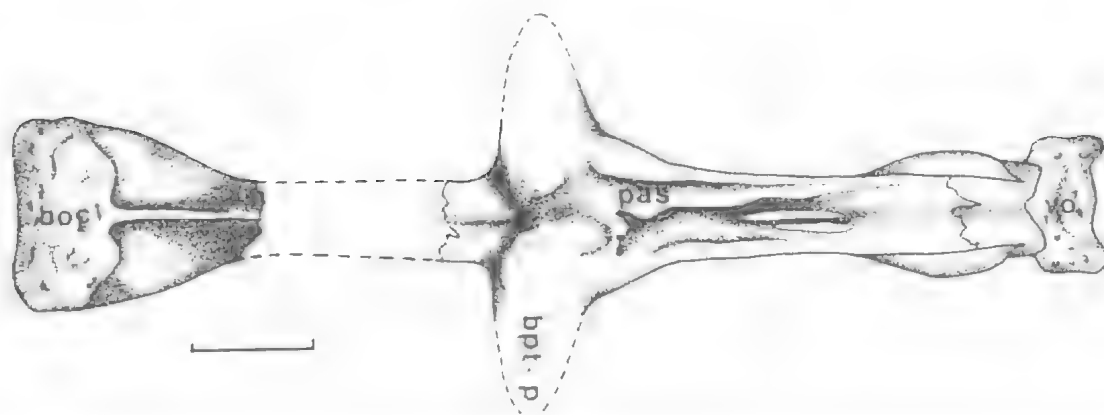


FIG. 2. Middle ventral part of the cranial base of †*Phareodus queenslandicus*, QMF2359a. Scale bar = 10mm.

opercle is distinctly concave. 2) The mandibuloquadrate articulation lies far behind the orbit. 3) The mouth cleft is strongly upturned (Greenwood & Patterson, 1967). 4) Hypurals are reduced to five. These four characters indicate that †*Singida* is more closely related to *Osteoglossum* and *Scleropages* than it is to other genera in Osteoglossomorpha.

Genus †*Phareodus* Leidy, 1873

Osteoglossum Cope, 1872: 429; *Phareodus* Leidy, 1873: 99; Thorpe, 1938: 287; Hills, 1934: 160-164; Roellig, 1967: 137; Taverne, 1978: 7; Grande, 1984: 69; *Phareodon* Leidy, Cope, 1873: 637; *Dapedoglossum* Cope, 1877a: 807; Cope, 1877b: 570; Cope, 1883: 68-73; *Phareoides* Taverne, 1973: 497-499; Taverne, 1974: 724-734.

TYPE SPECIES

†*Phareodus encaustus* (Cope, 1872) (= †*Phareodus acutus* Leidy, 1873).

INCLUDED SPECIES

†*Phareodus encaustus* (Cope, 1872), †*Phareodus testis* Leidy, 1973, †*Phareodus* (= *Phareoides* Taverne, 1973) *queenslandicus* Hills, 1934.

EMENDED DIAGNOSIS

Osteoglossinae differing from other genera in having the following features: frontal consisting of a narrow posterior portion and a laterally greatly expanded anterior portion, parasphenoid with teeth on posterior part, teeth on premaxilla ranging from 7 to 9 (never more than 9), depth to width of opercle ratio 2-2.5, first ual centrum bearing

two complete neural spines, TV = 47-51, DFR = 16-21, DP = 18-24, AFR = 22-28, AP = 22-28, H = 5-6, CFR = 1-8-7-1.

†*Phareodus queenslandicus* Hills, 1934 (Figs 1A; 2; 3; 4A-B; 5A; 6A; 7A)

Phareodus queenslandicus Hills, 1934: 160-164, text-figs. 3-7; Hills, 1958: 100; Roellig, 1967: 43-49, 143-144, figs. 17-21; *Phareoides queenslandicus* Taverne, 1973: 497-499, fig. 1; Taverne, 1978: 25-32, figs. 15-19; Taverne, 1979: 123.

DIAGNOSIS

†*Phareodus* differing from North American species mainly in having the combination of the following characters: suture between frontal and parietal antero-medially directed; dentary teeth about 27; ratio of depth to width of opercle about 2 to 2.5; origin of dorsal fin opposite origin of anal fin; TV = 46-49; DFR = 19; DP = 19; AFR = 26; AP = 26.

HOLOTYPE

QMF2357, a poorly-preserved specimen showing part of the cranial skeleton.

REFERRED SPECIMENS

QMF2917 (cast of UQF14960), incompletely showing the skull roof (Fig. 1A); QMF2359, poorly-preserved part and counterpart, showing some of the cranial skeleton; QMF5754, showing part of the cranial skeleton; QMF2361, a poorly-preserved caudal region showing some scales and incomplete caudal fin rays.

LOCALITY AND OCCURRENCE

Redbank Plains, southeastern Queensland, Australia; Lower Tertiary, Redbank Plains Formation; Eocene to Oligocene.

REMARKS

Hills (1934), Roellig (1967), and Taverne (1978) have given a rather detailed description of this species, providing this study with valuable information. It is not necessary to redescribe all of the structures which were noted by those authors. This paper will emphasize those characters that I think are the most important for the phylogenetic analysis.

DESCRIPTION

Skull roof. QMF2917 (cast of UQF14960) shows a relatively well-preserved skull roof (Fig. 1A). The mesethmoid is rhomboid in dorsal view, inserting posteriorly between the anterior ends of the two frontals. The frontal is similar to that in †*Phareodus encaustus*, in which it is at least twice as broad anteriorly as posteriorly (Fig. 1). As in †*Phareodus encaustus*, a "V-shaped" depression that receives the posterior end of the nasal is present on the anterior margin of each of the frontals (Fig. 1). The suture between the frontals is relatively straight anteriorly but sinuous posteriorly. The parietal is irregular in shape with a length approximately 1/3 of that of the frontal. The suture between the two parietals is also sinuous.

Unlike the two North American species, the suture between frontal and parietal is antero-medially directed.

As in †*Phareodus encaustus*, the dorsally crested supraoccipital does not extend anteriorly to separate the posterior portion of the parietals.

Middle ventral part of cranial base. Judging from the remains on QMF2359a, the cranial base is structurally similar to that in the North American †*Phareodus* species. It consists of the vomer, the parasphenoid, and the basioccipital.

The vomer is somewhat shovel-shaped in ventral view with teeth on its anterior part.

As in the two North American †*Phareodus* species, the parasphenoid resembles a sword and bears strong basipterygoid processes (Fig. 2). However, teeth may be absent from the ventral side of this bone in the Australian species.

Opercular series. The bones comprising this series in †*Phareodus queenslandicus* are individually nearly identical to those in †*Phareodus encaustus* in both shape and proportions. The preopercle (Fig. 3) is slightly curved



FIG. 3. Preopercle of †*Phareodus queenslandicus*, QMF2359a. Scale bar = 10mm.

with an indistinct horizontal arm on which the preoperculo-mandibular canal opens in a groove (a synapomorphy of the subfamily Osteoglossinae). The opercle is subsemicircular in shape with a depth to width ratio about 2-2.5 (Fig. 4A,B).

Posterior infraorbitals. The two infraorbitals behind the orbit are almost identical to those in †*Phareodus encaustus* (Fig. 5A,B), consisting of one shallow (lower) and one deep (upper) element. The lower one is considered to be the third infraorbital, and the upper one the fused fourth and fifth. As in other osteoglossids, these two posterior infraorbitals cover the entire postorbital area between the posterior edge of the orbit and the preopercle.

Jaws. Both the upper and the lower jaws are virtually identical to those of the two North American †*Phareodus* species (Fig. 6). The maxilla is slightly dorsally curved with a relatively deep posterior portion and a tapering anterior end that overlaps the posterior part of the premaxilla. As in †*Phareodus encaustus*, a distinct dorsal swelling is also present on the anterior portion of the maxilla at the level behind the premaxilla. At least 26 conical teeth can be counted on the

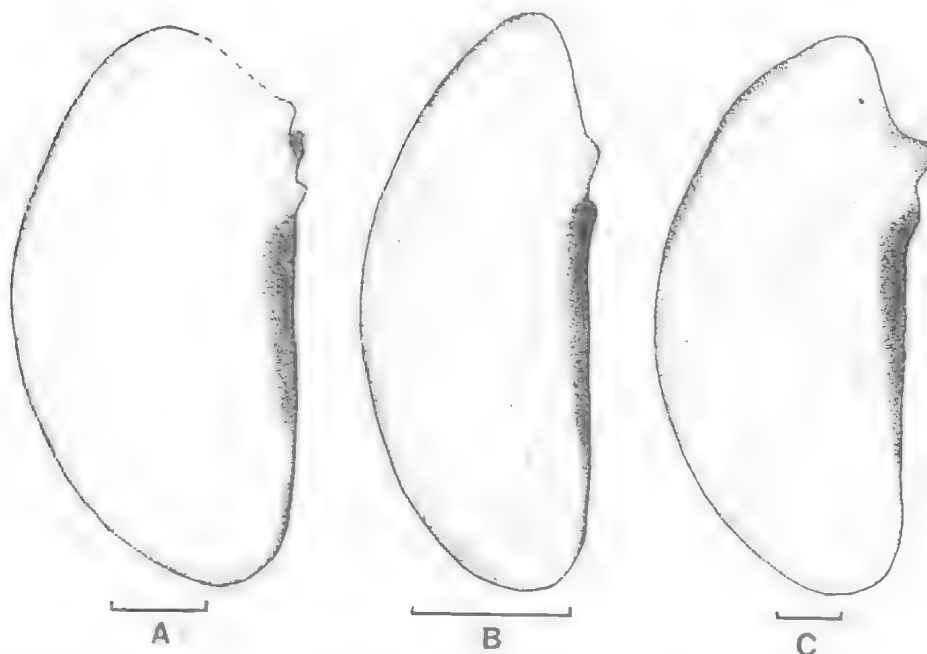


FIG. 4. Opercle. A,B, †*Phareodus queenslandicus*. A, QMF5754a; B, QMF2357. C, †*Phareodus encaustus*, FMNHPF12681. Scale bars: A, C = 10mm; B = 20mm.

maxilla of QMF2357. A supramaxilla is absent. Taverne (1978: 26, fig. 15) labelled a supramaxilla in his illustration, but I am doubtful about that identification.

The dentary gradually deepens posteriorly and has a moderate coronoid process. This bone bears about 27 conical teeth that are larger than those on the maxilla and arranged in at least two rows.

A mesial (internal) view of the lower jaw (QMF2357) suggests a large triangular angular posterior to the dentary. Mesially adjoining this bone are an articular, which is irregular in shape and thicker posteriorly than anteriorly, and a small coronomeckelian. The retroarticular is identifiable on QMF2357, in which it is postero-ventral to the articular and angular. As in the North American †*Phareodus* species, the articular is not fused with the angular, and the articular facet for the quadrate is mainly on the articular (Fig. 6) (also see Nelson, 1973).

Hyoid arch. A complete hyomandibular is preserved in QMF2359a. This bone has a single head articulating with the cranium, a long postero-ventrally directed process articulating with the opercle, and a subtriangular anterior wing extending anteriorly as far as to the posterior rim of the orbit. A strong vertical ridge on the shaft of the hyomandibular extends from the head

to the ventral tip where the bone articulates with the symplectic. This type of hyomandibular closely resembles that of †*Phareodus encaustus* (Fig. 7B).

DISCUSSION

SYNONYMY OF †*PHAREOIDES* WITH †*PHAREODUS*

When Taverne (1973: 497,498) established †*Phareoides*, he used 20 characters in its diagnosis: 1, Ostéoglossidé de grande taille (50cm), au corps court et trappu; 2, mâchoires ornées de grandes dents; 3, supraethmoïde hypertrophié; 4, naso-frontaux en contact médian; 5, expansions latérales externes de grande dimension dans la région naso-frontale; 6, pariétaux en contact médian et dénivelés en leur milieu; 7, ptérotiques étroits et très longs; 8, présence d'une fosse occipito-dorsale sur le pariétal, l'épiotique et le supraoccipital; 9, un supramaxillaire; 10, ptérygoïdes dentés; 11, hypertrophie des troisième et quatrième infraorbitaires; 12, préoperculaire haut et large, à branche ventrale très réduite; 13, operculaire étroit mais très haut; 14, museau raccourci; 15, mandibule large et remon- tante; 16, premier rayon pectoral beaucoup plus fort que les suivants; 17, nageoires dorsale et anale très reculée sur le corps; 18, une cinquantaine de

vertèbres; 19, vertèbres abdominales à grandes hémaphyses situées transversalement; 20, écailles grandes, ornées d'une fine granulation et à radii en structure réticulée.

Among the above features of †*Phareoides*, none can be said to be an autapomorphy of this genus in the family Osteoglossidae. Character (1) is present not only in †*Phareodus*, but also in the recent *Osteoglossum*, *Scleropages*, and *Heterotis* if we count both the juveniles and the adults. Moreover, such variation in body size is of doubtful significance because we do not know how large the largest individuals of this Australian fossil species could be.

Character (2) is definitely a plesiomorphy. It is present in all of the extant and fossil genera of Osteoglossiformes (Ridewood, 1904, 1905; Taverne, 1977, 1978, 1979) except †*Singida* (Greenwood & Patterson, 1967). Large teeth on the lower and upper jaws can also be seen in most of the genera of Hiodontiformes (e.g., †*Yanbiania* Li, 1987; †*Eohiodon* Cavender, 1966; and *Hiodon* Lesueur, 1818) and many other teleosts (Gregory, 1933).

Character (3) needs to be clarified. Taverne's so-called "supraethmoïde" is synonymous with Hills' (1934) "mesethmoid" or Kershaw's (1976) "dermethmoid". I prefer using Hills' term to Taverne's "supraethmoïde" in this paper. This character is in fact shared at least by the two North American †*Phareodus* species. It should also be noted that Taverne's restoration of the naso-eth-

moid region and his identification of the bones in this region of †*Phareodus acutus* [=†*Phareodus encaustus* (Cope, 1872)] is incorrect. My recent examination of numerous specimens referred to †*Phareodus* from North America indicates that there is no such bone called "supraethmoïde" at the position labelled by Taverne (1973: 498, fig. 1) in either †*Phareodus encaustus* or †*P. testis*. His so-called "nasal" is also likely misidentified. At the place where Taverne labelled a "nasal", I can find only one bone that shows an appearance similar to his so-called "supraethmoïde" in †*Phareoides queenslandicus* (see Fig. 1). The true nasals, which could have been either missing from the specimens (FMNHPP14262) or disarticulated with the adjacent bones (FMNHPP12683), are separated from each other by the subrhomboid mesethmoid in the two North American †*Phareodus* species (see Fig. 8). I am also doubtful of Taverne's (1973, 1974, 1978) restoration for †*Brychaetus muelleri* (see Woodward, 1901). Judging from the illustrations provided by Woodward, that western European species may be also similar to the two North American †*Phareodus* species in the above aspects (pers. obs.).

Characters (4) and (5) are also in need of clarification. Hills (1934) made a mistake in identifying the frontal as the fused nasal plus frontal and labeling the anterior extension of the frontal as the "nasal" of †*Phareodus queenslandicus*. Taverne (1973, 1978) modified Hills' mistake,

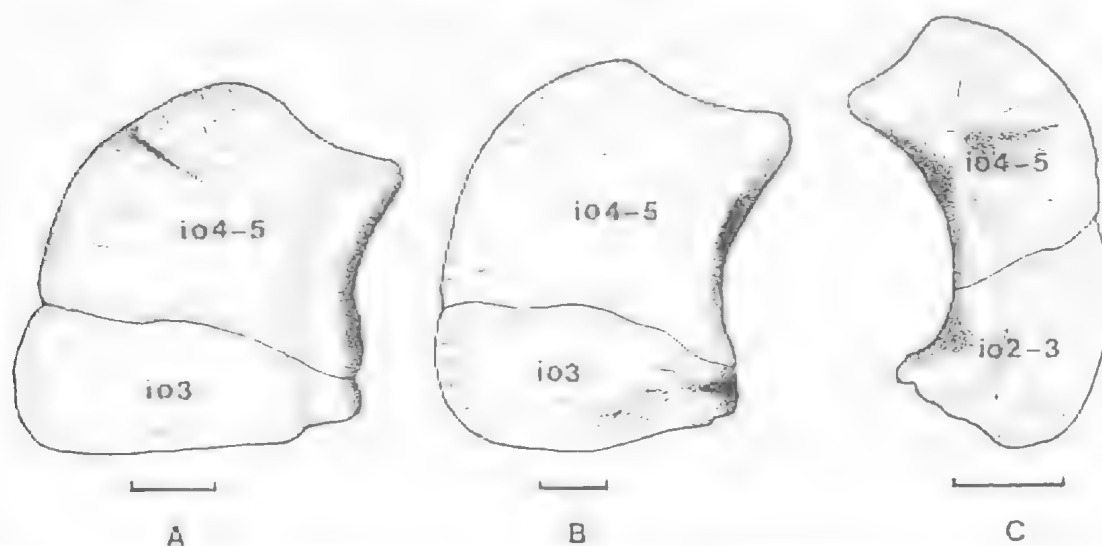


FIG. 5. Comparison of the posterior infraorbitals of †*Phareodus*. A, †*Phareodus queenslandicus*, QMF2351; B, †*Phareodus encaustus*, FMNHPP10256; C, †*Phareodus testis*, FMNHPP12682. Scale bars = 10mm.

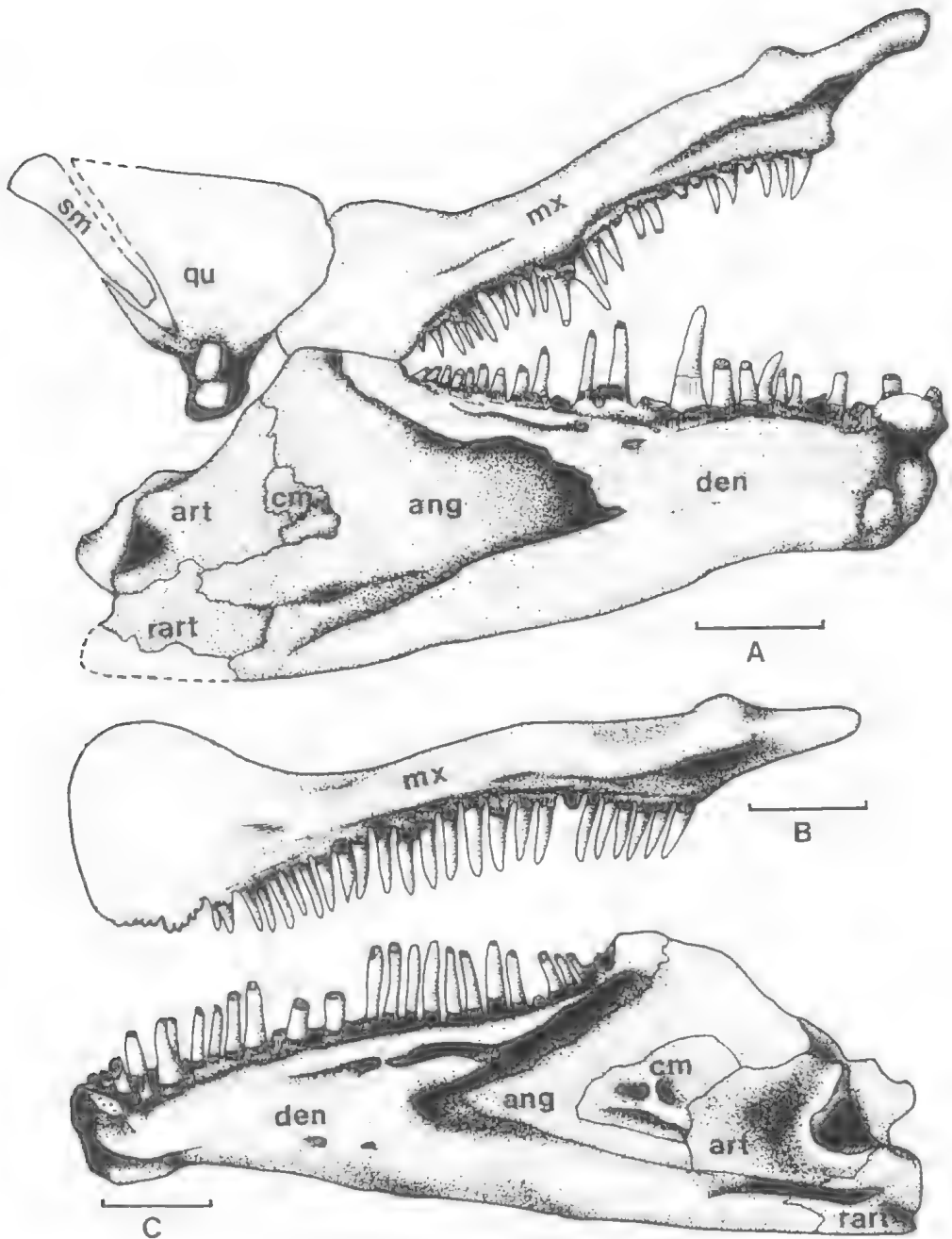


FIG. 6. Upper and lower jaws of †*Phareodus*. A, †*Phareodus queenlandicus*, QMF2357; B,C, †*Phareodus encaustus*. B, FMNHPF12683, C, AMNH2472. Scale bars = 10mm.

but he continued labeling the frontal and nasal as a fused “naso-frontaux” when he established †*Phareoides*. My study of the cast of UQF14960 suggests that the nasals are missing from the

imen, leaving only a “V-shaped” depression on the anterior margin of each of the frontals, and that the two nasals are also separated from each other by the mesethmoid in this fish. The part

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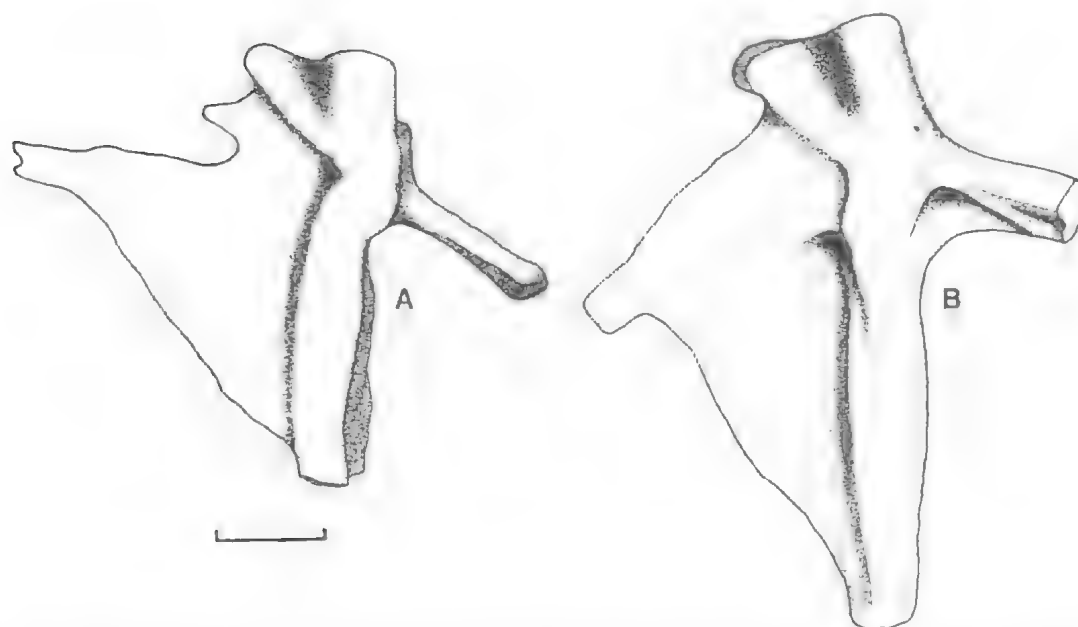


FIG. 7. Hyomandibular. A, †*Phareodus queenslandicus*, QMF2359a; B, †*Phareodus encaustus*, FMNHPP10285. Scale bar = 10mm.

labeled as the "nasal" by Taverne is, therefore, exactly the medio-anterior extension of the frontal (Fig. 1A). This situation is identical with that in the two North American †*Phareodus* species (see Fig. 1B). Therefore, Taverne's so-called "naso-frontaux" of †*Phareoides queenslandicus* consists only of the frontal. As illustrated by Taverne himself, the two frontals in †*Phareodus encaustus* and †*Brychaetus muelleri* are also medially sutured with each other and antero-laterally expanded. These two characters can thus only be considered to be synapomorphies shared by †*Phareodus*, †*Brychaetus*, and †*Phareoides*.

Character (6) is definitely not unique to †*Phareoides*. Parietals meeting with each other along the dorso-medial line can be seen at least in †*Phareodus*, †*Brychaetus*, the extant *Heterotis*, *Arapaima*, notoptyrids (Ridewood, 1904, 1905; Kershaw, 1976; Taverne, 1978), and all of the lycoperids and hiodontids (Ridewood, 1904; Greenwood, 1970; Taverne, 1977, 1978; Li, 1987; Li & Wilson, 1994). The only difference is that the suture between the two parietals is zig-zag-shaped in †*Phareoides* but nearly straight in the other genera mentioned above.

Character (7) refers to the pterotics. Although they are incompletely preserved on the specimen (Fig. 1A), the pterotics of †*Phareoides* are indistinguishable from those of the two North

American †*Phareodus* species (Fig. 1B). In addition, elongate pterotics can also be seen in †*Brychaetus* (Woodward, 1901; Roellig, 1974; Taverne, 1978) and in the extant *Arapaima* (Ridewood, 1905; Kershaw, 1976). It is evident that this character is not unique to †*Phareoides*.

Character (8) defines a dorso-occipital fossa on the parietal, epiotic, and supraoccipital of †*Phareoides*. A similar depression is also developed in †*Brychaetus* (Taverne, 1978) and the two North American †*Phareodus* species (see Fig. 1B).

Character (9) suggests the presence of one supramaxilla in †*Phareoides*. My examination failed to confirm this bone in the specimens referred to †*Phareoides*. I believe Taverne's so-called "supramaxillaire" could be the posterior part of the endopterygoid.

Character (10) is related to the palato-pterygoquadrate arch. In both the fossil and the extant osteoglossomorphs, toothed pterygoids (including ectopterygoid and endopterygoid) are commonly seen in most of the taxa of Osteoglossomorpha (Greenwood et al., 1966; Taverne, 1977, 1978). Therefore, †*Phareoides* can not be characterized by this plesiomorphy.

Character (11) describes the posterior infraorbitals of †*Phareoides*. In fact, †*Phareodus encaustus* shares this character with †*Phareoides*

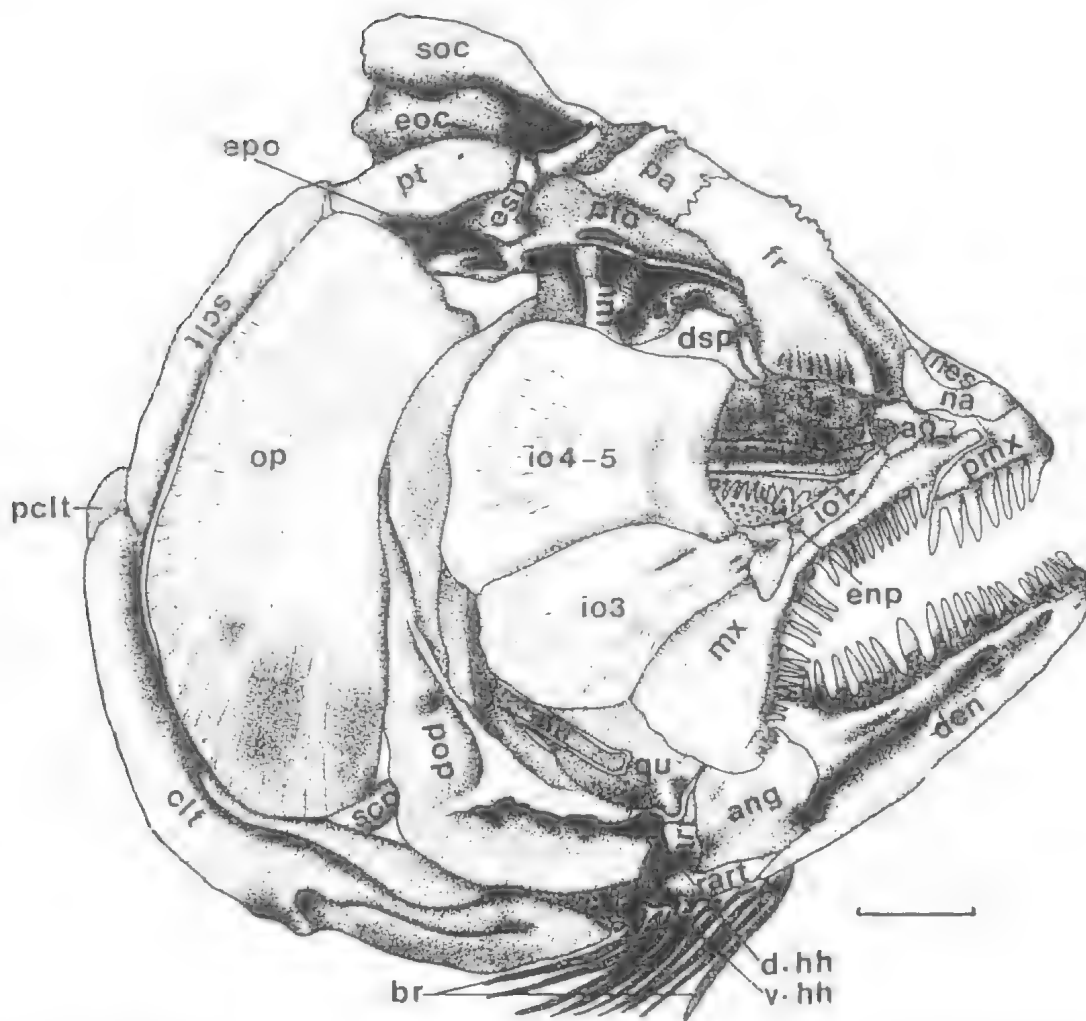


FIG. 8. †*Phareodus encaustus*. Line drawing of FMNH PF14040, showing the typical skull (cranial) characteristics of †*Phareodus*. Scale bar = 20mm.

(Fig. 5A-B). Similar posterior infraorbitals may also be seen in †*Brychaetus* (Woodward, 1901; Roellig, 1967, 1974; Taverne, 1978).

Characters (12) and (13) define the preopercle and opercle of †*Phareoides*. Using these two characters, I am not able to distinguish †*Phareoides* from all of the other genera grouped in the Osteoglossinae.

Character (14) is doubtful because the naso-oral region is poorly preserved on the specimens. Even if Taverne is correct, a reduced (short) naso-oral region can also be seen in the two North American †*Phareodus* species and the extant *Heterotis*.

Character (15) refers to the lower jaw. A detailed comparison suggests that the mandible in †*Phareoides* is almost identical with that in the two North American †*Phareodus* species in both structure and shape (Fig. 6).

Character (16) is one of the synapomorphies of the subfamily Osteoglossinae (Li, in press). Including †*Singida* (see Greenwood & Patterson, 1967), all of the genera in the subfamily possess a particularly strong first pectoral fin ray.

Character (17) is plesiomorphic for Osteoglossidae. Posteriorly located dorsal and anal fins are present not only in Osteoglossomorpha but also

TABLE 1. Comparison of †*Phareodus queenslandicus* with the two North American †*Phareodus* species, showing that all of the known meristic characters, as well as the ratio of opercular depth to opercular width, of †*Phareodus queenslandicus* are within the range of the two North American †*Phareodus* species.

| | † <i>Phareodus encaustus</i> | † <i>Phareodus testis</i> | † <i>Phareodus queenslandicus</i> |
|------------------------------|------------------------------|---------------------------|-----------------------------------|
| Precaudal Vertebrae | 22-25 (23) | 22-25 | ~23 |
| Caudal Vertebrae | 25-27 (26) | 24-28 | ~26 |
| Total Vertebrae | 47-51 (49) | 47-52 | ~49 |
| Branchiostegals | 9-10 (10) | 8-11 | ? |
| Pectoral Fin Rays | 7-10 | 7-10 | ~6 |
| Pelvic Fin Rays | 4-6 | 4-6 (6) | ~4 |
| Principal Dorsal Fin Rays | 17-22 | 16-20 (18) | ~19 |
| Dorsal Pterygiophores | 18-24 | 18-21 (19) | ~19 |
| Principal Anal Fin Rays | 22-25 | 24-28 (26) | ~26 |
| Anal Pterygiophores | 22-26 | 24-28 (26) | ~26 |
| Caudal Fin Rays | 17 | 17* | 16 |
| Hypural | 5-6 (5) | 5-6 (6) | ? |
| Epural | 1 | 1 | ? |
| Supraneural | 22-26 | 22-26 | ? |
| Neural Spine on U1 | 2 | 2 | ? |
| Neural Spine on Pu2 | 1 | 1-2 | ? |
| Uroneural | 0 | 0 | ? |
| Opercular Depth/Ocular Width | 2-2.50 | 2-2.58 | 2-2.50 |

Numbers in brackets represent the most common situation within the range.

*16 on FMNHPP13576.

in some relatively primitive euteleosts (e.g. Esocidae; Nelson, 1984, and pers. obs.).

Character (18), which gives the number of the vertebrae of †*Phareoides*, and (19), which defines the parapophyses, are shared also by the two North American †*Phareodus* species. My examination of the new North American fossils indicates that †*Phareodus encaustus* and †*P. testis* also have a vertebral column consisting of 47 to 51 centra (Table 1) and a pair of strong parapophyses on the abdominal vertebrae.

Character (20) describes the scales of †*Phareoides*. Reticulate scales with fine granular ornament are seen in all of the extant genera of Osteoglossidae (Lauder & Liem, 1983; Greenwood et al., 1966; Taverne, 1977, 1978) and in fossil †*Phareodus* (Cope, 1872, 1873; Leidy, 1873; Thorpe, 1938; Grande, 1984) and †*Sinoglossus* (Su, 1986).

To sum up, Taverne's diagnosis for †*Phareoides* does not characterize that genus. It is only a list of characters of †*Phareodus* mixed with characters of the family Osteoglossidae, the superorder Osteoglossomorpha, and other primitive teleosts. In fact, †*Phareoides* and †*Phareodus* are indistinguishable from each other in all of the 20 characters. This indicates that †*Phareoides* Taverne 1973 is a junior synonym of †*Phareodus* Leidy 1873.

PHYLOGENY OF †*PHAREODUS QUEENSLANDICUS*

Grande's (1984) study and my recent reexamination suggest that †*Phareodus* contains only two valid North American species: †*Phareodus encaustus* and †*P. testis*. The difference between these two North American species seems to be greater than the difference between †*Phareodus queenslandicus* and †*P. encaustus* (Table 1). Moreover, †*Phareodus queenslandicus* appears to be phylogenetically more closely related to †*P. encaustus* than it is to †*P. testis*. This hypothesis is supported by the following character states:

1. Anterior portion of frontal greatly expanded laterally. The frontal in †*Phareodus queenslandicus* is almost identical to that in †*Phareodus encaustus* in shape. In these two species the frontal has an anterior portion that is greatly expanded laterally, with a width at least twice as great as that of the posterior portion, or 1/2 of the length of this bone (Fig. 1). A frontal similar to that in †*Phareodus queenslandicus* and †*Phareodus encaustus* was supposed to be present in †*Brychaetus muelleri* by Roellig (1967, 1974) and Taverne (1978). My study suggests that there are too many discrepancies between Taverne's restorations and Woodward's (1901) original illustrations for that species. That makes me doubtful about Taverne's description of the frontal in †*Brychaetus muelleri*.

It is true that the frontals in some other osteoglossiforms (Greenwood & Patterson, 1967; Roellig, 1967; Kershaw, 1976; Taverne, 1977, 1978; Grande, 1984) are also anteriorly broader than posteriorly; however, none of them has an anterior portion twice as broad as the posterior portion (pers. obs.).

2. Hyomandibular with a stick-like opercular process and a subtriangular anterior wing.

Among the previously named fossil osteoglossids, such a hyomandibular has been seen so far only in †*Phareodus queenslandicus* (QMF2359 = RP/B-1 in Hills, 1934) and †*Phareodus encaustus* (Fig. 7). The stick-like opercular process in these two species is particularly long and forms an approximately equal angle with the lower vertical ridge of the hyomandibular. The subtriangular anterior wing extends anteriorly to the posterior edge of the orbit, ending in a distinct process that connects with the endopterygoid.

The hyomandibular in †*P. testis* bears a shorter opercular process but no distinct subtriangular anterior wing like that in the other two species.

3. Dentary bearing almost the same number of teeth. As shown in Figure 6, the dentary in both †*Phareodus queenslandicus* and †*P. encaustus* bears 27 large conical teeth. This coincidence can not be interpreted as a simple similarity between these two species. Most of the specimens referred to †*Phareodus encaustus* have 25 to 27 dentary teeth. This is also the estimate of the number of dentary teeth in †*Phareodus queenslandicus*. The teeth on the dentary of †*P. testis* are usually three to four fewer than those of the above two species. It seems to me that the number of dentary teeth may be phylogenetically informative although this significance should be further investigated.

4. Preopercle with an indistinct horizontal arm. In †*Phareodus queenslandicus*, the preopercle is moderately curved, with the upper part approximately as broad as the lower part (Fig. 3). No distinct horizontal arm can be seen in this species. This type of preopercle is basically the same as that in †*Phareodus encaustus* (Fig. 8). Although the preopercles in †*P. testis* (e.g. UALVP17658) and the extant *Osteoglossum* (e.g. UAMZ4642) are also shallowly curved in shape, they possess a distinct horizontal arm and a dorsally tapered vertical arm. Thus a moderately curved preopercle without a distinct horizontal arm may be another important character state linking †*Phareodus queenslandicus* with †*P. encaustus*.

5. Posterior infraorbitals (io3 and io4+5) in the same pattern. QMF2357 (Fig. 5A) and QMF5754 show two posterior infraorbitals of †*Phareodus queenslandicus*. The narrower lower one was considered to be the third infraorbital, and the broader upper one the fourth by Taverne (1978: 26, fig. 15). Among the other known osteoglossomorphs (Nelson, 1969), similar posterior infraorbitals are present only in †*P. encaustus* and possibly in †*Brychaetus* (pers. obs.). As shown

(Figs 5, 8) †*Phareodus queenslandicus* and †*P. encaustus* are indistinguishable from each other in the pattern of the posterior infraorbitals.

CONCLUSIONS

1. Taverne's diagnosis for †*Phareoides* is only a list of characters of †*Phareodus* mixed with characters of the family Osteoglossidae and the superorder Osteoglossomorpha. In fact, †*Phareoides* and †*Phareodus* are indistinguishable from each other in all of the 20 characters listed in the diagnosis, indicating that †*Phareoides* is a junior synonym of †*Phareodus*.

2. The Australian †*Phareodus queenslandicus* is phylogenetically most closely related to †*P. encaustus* from North America. This relationship is mainly supported by the frontal consisting of a narrow posterior portion and a greatly expanded anterior portion, the hyomandibular bearing a stick-like opercular process and a subtriangular anterior wing, the number of the dentary teeth, the preopercle with an indistinct horizontal arm, and the pattern of the posterior infraorbitals.

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AERIAL OBSERVATIONS OF LARGE ZIPHIID WHALES, POSSIBLY *BERARDIUS ARNUXII*, OFF THE SOUTHERN COAST OF NEW SOUTH WALES

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Paterson, R.A. & Parker, A.E. 1994 12 01: Aerial observations of large ziphiid whales, possibly *Berardius arnuxii*, off the southern coast of New South Wales. *Memoirs of the Queensland Museum* 37(1):301-306. Brisbane, ISSN 0079-8835.

Large ziphiid whales incidentally observed during tuna-spotting operations on the continental slope of the NSW coast between 34°-37°S are tentatively identified as *Berardius arnuxii*. Morphology, school structure, location and month of sighting are compared with available data for the species together with those for *B. bairdii*, its sole congener, which is confined to the North Pacific Ocean. □ *Large ziphiids, aerial observation, New South Wales.*

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Detailed accounts of behaviour and school structure of ziphiids are limited with the exception of *Berardius bairdii* and *Hyperoodon ampullatus*, exploited species found in the North Pacific and North Atlantic Oceans respectively. Details are reported here of large ziphiids, tentatively identified as *Berardius arnuxii*, incidentally observed off the southern New South Wales (NSW) coast by one of us (AEP) while employed as a tuna-spotting pilot between 1961 and 1987.

OBSERVATIONS

The data are summarised (Table 1) with the exception of a sighting made during a familiarisation flight in January 1962 (Fig. 1). The absence of sightings between 1963 and 1980 is considered to reflect the timing of flying operations in those years. While catches of the preferred target species (southern bluefin tuna) were substantial, flying in NSW ceased by early December and



FIG. 1. School of large ziphiids off the southern NSW coast, January 1962.

TABLE 1. Sightings of large ziphiid whales off the southern New South Wales Coast.

| Date | Time (if applicable) | Position | Number | Estimated length(m) |
|----------|----------------------|------------------|-------------|---------------------|
| 24.1.81 | 1400 | 35°46'S 150°38'E | 12 | 7.5 |
| 24.1.81 | 1435 | 35°50'S 150°51'E | 4 | 7.5 |
| 26.1.81 | 1445 | 35°47'S 150°40'E | 4 (2 pairs) | 4.5 & 6.0 |
| 26.1.81 | 1515 | 36°06'S 150°30'E | 3 | |
| 19.11.81 | | 36°36'S 151°37'E | 2 | 5.5-6.0 |
| 29.11.81 | | 36°42'S 152°39'E | 2 | 5.5 |
| 10.12.81 | | 36°01'S 150°27'E | 7-8 | 6.0 |
| 9.1.82 | | 35°22'S 150°58'E | 6 | 6.5 |
| 2.1.84 | | 35°25'S 150°53'E | ~6 | |
| 3.1.84 | | 36°13'S 150°34'E | 6 | 9.5-10.0 |
| 7.1.84 | 0910 | 36°49'S 150°24'E | >8 | |
| 7.1.84 | 1035 | 36°50'S 150°24'E | ~6 | |
| 7.1.84 | 1240 | 36°57'S 150°21'E | >8 | |
| 9.1.84 | | 35°23'S 150°56'E | ~5 | |
| 9.1.84 | 1510 | 36°00'S 151°09'E | 1 | 6.0 |
| 9.1.84 | 1520 | 34°52'S 151°17'E | 4 | 7.5-9.0 |
| 9.1.84 | 1600 | 36°17'S 151°09'E | 4 | 7.5-9.0 |
| 11.1.84 | | 35°44'S 150°40'E | 6 | 7.5-9.0 |
| 12.1.84 | | 37°05'S 150°25'E | | |
| 19.1.84 | 0940 | 34°38'S 151°16'E | 4 | 9.0 |
| 19.1.84 | 1050 | 36°10'S 150°28'E | ~6 | |
| 23.1.84 | 1000 | 35°18'S 151°00'E | 4 | >9.0 |
| 23.1.84 | 1145 | 36°38'S 150°23'E | 4 | 9.0 |
| 2.2.84 | 1025 | 34°32'S 151°24'E | 10 | 7.5-9.0 |
| 2.2.84 | 1030 | 34°39'S 151°19'E | 2 | 6.0-7.5 |
| 2.2.84 | 1050 | 35°12'S 151°09'E | 9 | 6.0-7.5 |
| 4.2.84 | | 35°42'S 150°45'E | 16 | 7.5-9.0 |

operations were transferred to South Australia. However, as NSW bluefin catches declined in the early 1980s flights were continued often until March in attempts to locate other tuna species, such as skipjack, believed to be more abundant when sea temperatures were higher (21°-27°C). Flights were restricted in 1983 due to adverse weather and were reduced after 1984 due to further catch decline. AEP ceased flying in the region in 1987.

With few exceptions sightings were made in the relatively narrow area of the continental slope between 34°-37°S (Fig. 2) although flights were made for considerable distances beyond that area. All positions were determined by VLF/Omega navigational equipment. Sighting cues included breaching (Fig. 1), surface splashing and "tight finger" formation (Fig. 3) considered most char-

acteristic of undisturbed activity. The whales usually dived when approached and swam rapidly and unidirectionally for periods of up to twenty minutes beneath the surface while maintaining close formation. This relatively shallow depth of travel was unique amongst all whale species observed by AEP. Fluke raising was not observed on any occasion.

With the exception of two pairs seen on 26.1.81 members of each group were of similar length and calves were not identified. Dorsal scarring and a prominent anterior white area on the rostrum were noted when the whales were at the surface (Fig. 4). They were brown on the dorsum although some were paler perhaps due to more extensive scarring.

IDENTITY

As aerial observation was the only means of inspection the precise identity of these whales remains uncertain but their body length and well-defined rostrum indicate large ziphiids. On the basis of morphology, school structure, location and months of sighting we tentatively conclude that they were *Berardius arnuxii*. In reaching this conclusion reliance has been placed on comparable data, including aerial observations, available for *B. bairdii* the sole congener of *B. arnuxii*, which is confined to the North Pacific Ocean.

MORPHOLOGY

The length estimates are consistent with those of *B. arnuxii* reported by McCann (1975) but they overlap with *Hyperoodon planifrons*, *Mesoplodon layardii*, *Tasmacetus shepherdi*, *Ziphius cavirostris* and probably with *Indopacetus pacificus* which has never been reported in the living state. The "overhanging" melon and relatively short rostrum of *H. planifrons* tend to exclude it as the likely species. However, sightings of *H. planifrons* were reported in the study area at 34°19'S, 151°12'E on 30 February 1988 (Lewis, 1988). The observation that all members of each group were of similar length supports *B. arnuxii* in which adult males and females are of equal length (McCann, 1975). However, segregation of the sexes for *B.*

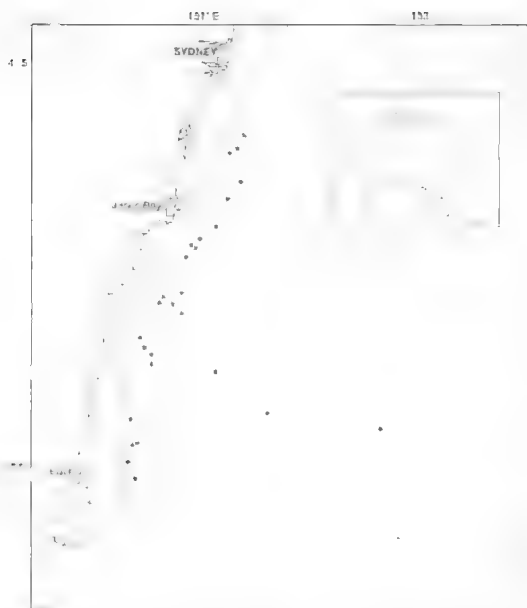


FIG. 2. Map of the southern NSW coast indicating position of large ziphiids from Table 1. The 200m isobath is shown.

bairdii has been noted by Leatherwood et al. (1982) and Balcomb (1989).

In *Berardius*, alone amongst ziphiids, functional anterior mandibular teeth (Fig. 5) erupt in both sexes (Moore, 1968). It is likely that the anterior white areas observed in the NSW ziphiids were teeth.

The brown dorsal colouration is consistent with the observations of Balcomb (1989) and with the colour illustration (McCann, 1975) of an elderly male *B. arnuxii* stranded at Pukerua Bay, New Zealand. Other colour descriptions vary from "dark" to black (Hale, 1939; McCann, 1975). However, those descriptions were of dead or dying animals (although so was the Pukerua Bay specimen) and it is possible that colour darkened due to terminal or post-mortem changes. Loughlin & Perez (1985) state that light conditions may result in colour variation and note that *Physeter macrocephalus* and *B. bairdii* which are neutral grey in colour appear dark brown in sunlight and greenish when submerged.

Miyashita (pers. comm.) considers that the NSW ziphiids belong to the genus *Berardius* because inter alia there is evidence of anterior convex configuration of the blow hole (which is unique amongst ziphiids) best seen in Fig. 6. However, we consider that film quality is insufficient to confirm such detail absolutely.

SCHOOL STRUCTURE

There is considerable similarity between the schools identified here and those of *B. bairdii* observed aurally off Japan. Kasuya (1971) noted school size of *B. bairdii* between 1-30 with a mean of 4.5. Shipboard estimates of school size of the same species were 1-25 with a mean of 7.5 (Kasuya, 1986). The NSW schools ranged between 1-16 with a mean of 5.8. Balcomb (1989) observed a large school of approximately 80 *B. arnuxii* in Robertson Bay, Antarctica in February 1986. That school later split into sub-groups of 8-15. His description of close proximity, dive sequences and non-raising of the flukes is similar to the NSW observations.

LOCATION AND MONTHS OF OBSERVATION

Previous data from Australasia (Hale, 1939; McCann, 1975) indicate that most *B. arnuxii* strandings occur during the summer months of December-March. In addition, a male *B. arnuxii* measuring 10.06m in length stranded at Cape Riche (34°42'S, 118°36'E) on 1 January 1989. The skull (WAMM29335) is held in the Western Australian Museum. The data in Table 1 are restricted to summer and *B. bairdii* also exhibits



FIG. 3. School of large ziphiids at 37°05'S, 150°25'E on 12 January 1984. "Tight finger" formation is evident. (Photograph taken from ~500m and subsequently enlarged).



FIG. 4. School of large ziphiids at 35°12'S, 151°09'E on 2 February 1984 showing dorsal scarring and anterior white areas considered to be teeth. Low "bushy" blows are also evident.



FIG. 5. Dentary of *B. arnuxii* (Samm5012) demonstrating the prominence of the anterior pair of mandibular teeth and the protrusion of the mandible in relation to the rostrum.

a summer peak in Japanese waters (Omura et al., 1955; Nishiwaki & Oguro, 1971) with movement into northern waters during cooler months. Kasuya (1971, 1986) noted absence of *B. bairdii* from Japanese coastal waters during the northern winter months of January–April. The NSW sightings were concentrated on the continental slope between 34°–37°S and *B. bairdii* concentrate on the continental slope of eastern Japan between 34°–38°N (Kasuya, 1971).

McCann (1975) considered that *B. arnuxii* approached the coastal waters of New Zealand in the summer months to breed. AEP is experienced in identifying calves and estimating the lengths of other cetaceans (Paterson, 1982) but did not identify calves in the schools observed off NSW.

CONCLUSION

The evidence concerning *B. arnuxii* so ably assembled and presented by McCann (1975) together with the observations of Balcomb (1989) in Antarctica and the data for *B. bairdii* support the likely identity of the NSW ziphiids as *B. arnuxii*. It is admitted that the absence of a specimen introduces tantalising uncertainty and that the estimated lengths of these ziphiids include species other than *B. arnuxii*. Future aerial and shipboard studies may result in more precise photo-identification and skin biopsy for DNA evaluation.

ACKNOWLEDGEMENTS

We owe particular thanks to Mr Tomio Miyashita of the Far Seas Fisheries Research Laboratory, Japan for his helpful advice. Dr Catherine Kemper of the South Australian Museum kindly provided the photograph of the dentary of the *B. arnuxii* held in the Museum's collection and Mr John Bannister, formerly Director of the Western Australian Museum, allowed us to examine specimen WAMM29335. Messrs Gary Cranitch and Bruce Cowell of the Queensland Museum prepared the photographs.

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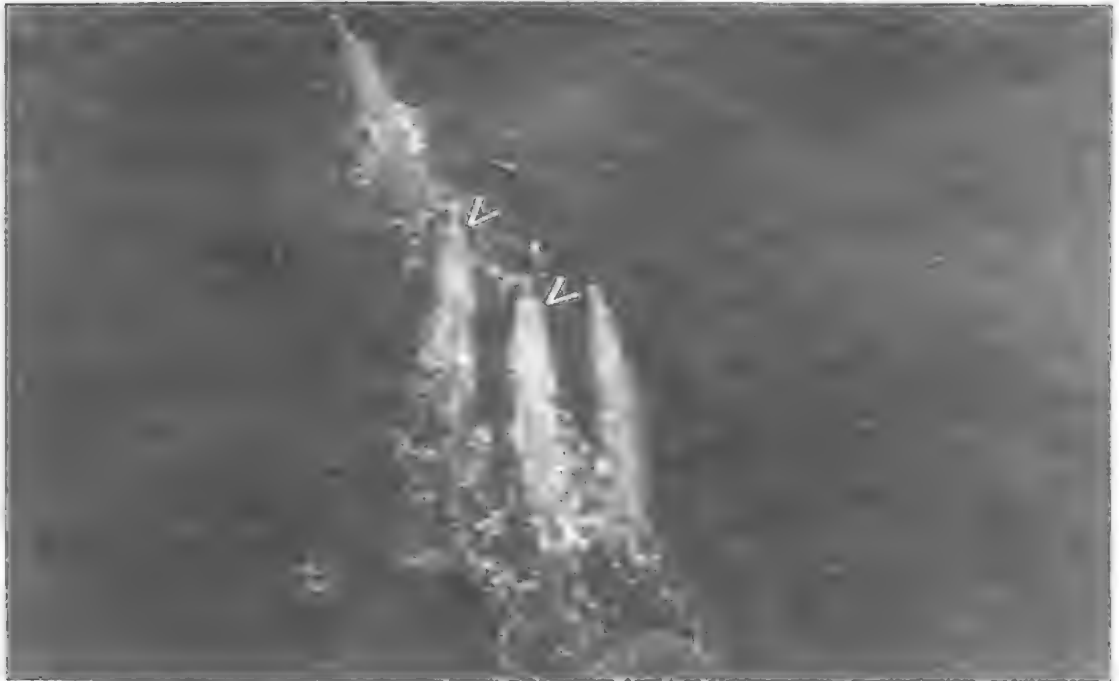


FIG. 6. Four large ziphiids at 34°38'S, 151°16'E on 19 January 1984. Possible anterior convex configuration of blow hole (arrows).

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A NEW SPECIES OF *COPHIXALUS* (ANURA: MICROHYLIDAE) FROM NORTHERN QUEENSLAND

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Richards, S.J., Dennis, A.J., Trenerry, M.P. & Werren, G.L. 1994 12 01: A new species of *Cophixalus* (Anura: Microhylidae) from northern Queensland. *Memoirs of the Queensland Museum* 37 (1):307-310. Brisbane, ISSN 0079-8835.

Cophixalus monticola sp. nov. is described from high elevation (> 1100m a.s.l.) rainforest on the Carbine Tableland, northern Queensland. Morphologically, it is similar to *Cophixalus concinnus* with which it occurs in sympatry. It differs from *C. concinnus* and all other Australian congeners in having a mating call that is a short trill lasting about 0.6s. □ Frog, new species, Microhylidae, *Cophixalus monticola*, upland rainforest.

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Microhylid frogs in Australia reach their greatest diversity in the Wet Tropics Biogeographic Region of northern Queensland. Twelve of 16 described species are found only in the narrow strip of tropical rainforest between Cooktown in the north and Mount Elliot near Townsville in the south (McDonald, 1992; Zweifel, 1985). Several species are widespread in this region (e.g. *Cophixalus ornatus*, *Sphenophryne fryi*) but others have restricted distributions, often associated with upland rainforest refugia (McDonald, 1992). Morphologically, Australian microhylids are extremely conservative and mating call has been an important tool in defining a number of species (Zweifel, 1985).

The Carbine Tableland of northern Queensland supports the most diverse assemblage of microhylid frogs in Australia including three *Cophixalus* and two *Sphenophryne* species (Zweifel, 1985). One of these species, *Cophixalus concinnus*, was originally described from Thornton Peak (Tyler, 1979) but had been collected previously from Mt Spurgeon on the Carbine Tableland (Zweifel, 1985). During research with Mr Garry Werren on the Carbine Tableland in the summer of 1985-86, Mr Andrew Dennis and Mr Michael Trenerry recognised a previously unknown species of *Cophixalus* that produced a short trill unlike the mating call of any other Australian *Cophixalus*.

The new species lacks clavicles and procoracoids, and the supplementary slip to its m.intermandibularis is narrow and runs parallel to the mandible. Both of these data indicate that the species belongs to *Cophixalus* and not to

Sphenophryne, the only other microhylid genus found in Australia (Burton, 1984).

Although morphologically similar to *C. concinnus* the call of this species is unlike the slow rattle described for a paratype of *C. concinnus* (Zweifel, 1985). Here we describe and illustrate the new species.

Specimens are lodged in the Queensland Museum (QM). Methods of measurement (in millimetres) follow Zweifel (1985). SVL=snout-vent length; TL=tibia length; EN=eye-naris; IN=internarial distance; HW=head width; ED=eye diameter.

SYSTEMATICS

Cophixalus monticola sp. nov. (Figs 1, 2)

MATERIAL EXAMINED

HOLOTYPE: QMJ58727, adult male, collected by S. Richards & A. Dennis, Carbine Tableland, 16°30'38"S, 145°16'18"E, altitude 1180m, 6.xii.93.

PARATYPES: QMJ58728-9 same data as for holotype; QMJ58730-1, M. Trenerry, G. Werren, 4.i.89; QMJ58732, M. Trenerry, G. Werren, 2.i.89; QMJ58733, QMJ58854, M. Trenerry, G. Werren, 30.i.88; QMJ58855-6, M. Trenerry, G. Werren, 13.i.88; QMJ58857, A. Dennis, M. Trenerry & G. Werren, 2.i.87; QMJ58871-3, A. Dennis, M. Trenerry, G. Werren, 12.xii.86; QMJ58874, A. Dennis, M. Trenerry, G. Werren, 5.i.86. All paratypes collected at altitudes over 1100m along a 4km stretch of Mt Lewis Rd at the type locality.

DIAGNOSIS

Distinguished from all known Australian congeners by a combination of the following charac-



FIG. 1. *Cophixalus monticola*, male, Carbine Tableland, northern Queensland.

ters: moderate size (males 17.3-21.2), tympanum indistinct, hind legs short (TL/SVL 0.37-0.41), mating call a short trill.

DESCRIPTION OF HOLOTYPE

An adult male with the following measurements. SVL 19.5; TL 8.0; EN 1.3; IN 1.6; SN 0.5; HW 7.6; ED 2.3; disc of third finger 0.9 (penultimate phalange 0.5); disc of fourth toe 0.9 (0.6).

Snout bluntly rounded in dorsal view, slightly projecting in profile; canthus rostralis rounded, loreal region steep, nearly vertical; nostrils lateral, much closer to tip of snout than to eye (EN/SN 2.6). Internarial distance greater than eye to naris distance (EN/IN 0.8), tympanum scarcely visible. Relative lengths of fingers 3>4>2>1, first finger very short; disc of first finger small, disc-like but not expanded, grooved terminal discs on second to fourth fingers well developed. Subarticular tubercles low, indistinct, no metacarpal tubercles. Toes unwebbed, relative lengths 4>3>5>2>1, all toes with grooved discs but disc on first toe rather poorly developed. Subarticular tubercles low, indistinct. Skin smooth dorsally and ventrally.

In preservative brown dorsally with scattered pale pink markings concentrated in the mid-line. Two pale lumbar ocelli evident. Dorsal pigmentation more diffuse laterally and on ventral surface of limbs. Central portion of venter white, bordered laterally and separated from lateral pigmentation by two broken, ventrolateral lines of dark pigment. Two indistinct pinkish bars behind eyes. No postocular stripe.

VARIATION

The paratypes are adult males with the following selected measurements and proportions: SVL 17.3-21.2; TL 6.9-8.1; HW 6.9-8.0; EN 1.3-1.55; IN 1.5-1.8; TL/SV 0.37-0.43; EN/IN 0.76-1.0. Colour in life is variable dorsally, ranging from red-brown through tan to yellow-brown, often with darker mottling on the back and legs, and there may be a broad pale vertebral stripe or a dark bar behind the eye. All of the types had two pale lumbar ocelli and ventrally were uniform pale yellow, red-brown, or white, with a darker throat region. Scattered dorsal tubercles are evident in some specimens (Fig. 1).

MATING CALL

The mating call of this species is a short trill. A single mating call of each of 10 different frogs recorded at 18-19.8°C had the following parameters: dominant frequency 2.5-3.0 KHz; duration 0.44-0.66s; pulse rate 23.3-41.0 pulses/s. A typical call recorded 6.xii.93 is presented in Fig. 2A (QMJ58729). The pulse rate increases sharply towards the end of this call but some calls did not exhibit this change in pulse rate. For comparison mating calls of two sympatric *Cophixalus*, *C. hosmeri* and *C. concinnus*, recorded at the type locality are presented (Fig. 2B,C). These were recorded on the same night

and at the same air temperature (17.8°C) as that presented for *C. monticola* (Fig. 2A).

Zweifel (1985) has discussed variation in calls of *C. concinnus* and *C. hosmeri* and noted that calls of Carbine Tableland *C. concinnus* closely resemble those described for one of the paratypes of that species collected on Thornton Peak. The calls of *C. hosmeri* and *C. concinnus* are a series of rather sharp 'clicks' or 'taps' differing in pulse rate and call length, and have an acoustic affect quite unlike the trill of *C. monticola*. The call of *C. concinnus*, the only species likely to be confused with *C. monticola*, is a slow tapping call lasting about 1-2 seconds and with a pulse rate of only 8-12/s (Zweifel, 1985). However the sug-

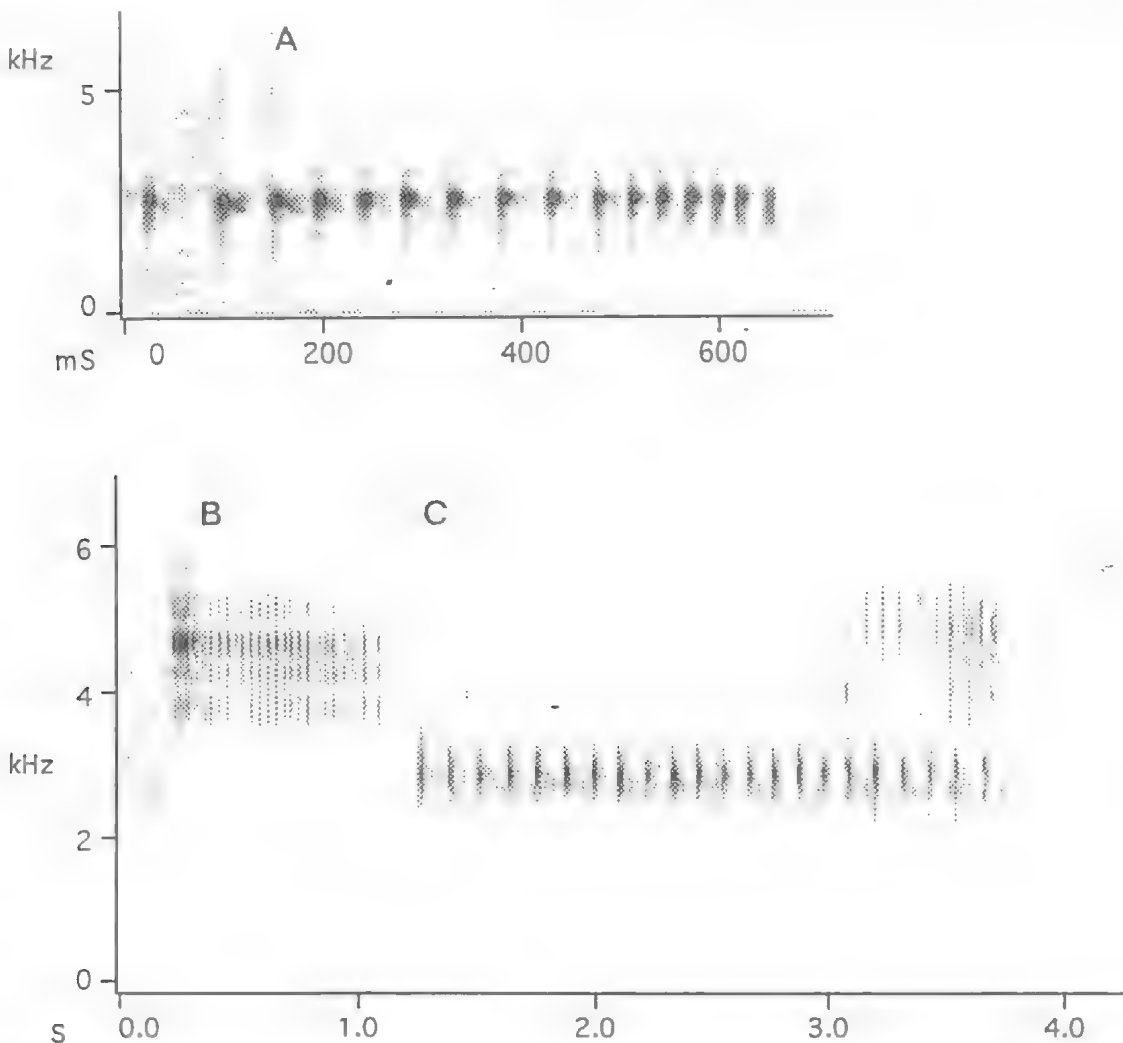


FIG. 2. Mating call. A, *Cophixalus monticola*; B, *Cophixalus hosmeri*; C, *Cophixalus concinnus*. Recorded on the Carbine Tableland, northern Queensland, 6.xii.93. Air temperature = 17.8°C.

gestion of Zweifel (1985) that the pulse rate of *C. hosmeri* is slower than *C. concinnus* at corresponding temperatures is incorrect, the opposite being true (Fig. 2; pers. obs.).

DISTRIBUTION AND HABITAT

Cophixalus monticola is known only from elevations above approximately 1100m on the Carbine Tableland. Males call from elevated perch sites, most commonly on *Linospadix* plants, up to 1.5m above the ground in closed-canopy rainforest. The paratypes were collected from the leaf axils of *Linospadix* palms (5), under the bark or in crevices of fallen trees or branches (5), from saplings (2), amongst roots projecting from a road embankment (1) and from a crevice in a large boulder in a dry creek bed (1). All specimens were 20–120cm above the substrate. Other specimens were calling from elevated positions in *Hemholtzia acorifolia* plants, and small *Oraniopsis appendiculata* palms. There appears to be a distinct difference in calling site preference between *C. monticola* and *C. concinnus*. The latter species was not found calling from these palms but usually called from sites no higher than 0.5m, commonly from litter on the forest floor. Calling *C. concinnus* are rather uniformly distributed throughout the forest floor, while *C. monticola* are more conspicuous in areas where the understorey is dominated by *Linospadix* palms.

On the morning of 7.xii.93 an unattended clutch of thirteen unpigmented eggs was found in the axil of a *Linospadix* plant. *C. monticola* had been calling from this area the previous night and the clutch almost certainly belongs to this species because other sympatric species were not calling from these plants. The eggs were in a small clump under accumulated litter in the leaf axil, and were joined by a thin but strong mucilaginous cord as described for *Cophixalus ornatus* (Zweifel, 1985).

COMPARISONS

Morphologically, this species is similar to *C. concinnus*, from which it is distinguished by its mating call. *C. mcdonaldi*, *C. neglectus*, *C. ornatus* and *C. peninsularis* are similar in size to *C. monticola*. Zweifel (1985) has presented a

detailed morphological comparison of these species with *C. concinnus* that will serve to distinguish these species from *C. monticola*. In addition these species, except *C. mcdonaldi*, a geographically isolated species over 300km from the known range of *C. monticola*, have mating calls quite different from the new species. The call of *C. mcdonaldi* remains unknown.

ETYMOLOGY

From the Latin *monticola* = dweller in the mountains, referring to the species' high-mountain habitat.

ACKNOWLEDGEMENTS

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THE KAKADU DUNNART, *SMINTHOPSIS BINDI* (MARSUPIALIA: DASYURIDAE).
A NEW SPECIES FROM THE STONY WOODLANDS
OF THE NORTHERN TERRITORY

S. VAN DYCK, J.C.Z. WOJNARSKI AND A.J. PRESS

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Sminthopsis bindi sp. nov. is described from the stony woodlands of the 'Top End' of the Northern Territory, Australia. This small-sized species with striate apical granules on the unfused interdigital pads of the hindfeet, closely resembles *S. archeri* and *S. butleri*. It is distinct, however, for its development of entoconids on the lower molars. Cladistic analysis suggests the affinities of *S. bindi* lie most closely with the *S. archeri*, *S. butleri*, *S. virginiae*, *S. douglasi* sub-clade. □ *Sminthopsis bindi*, dunnart, Kakadu National Park, Northern Territory, dasyurid.

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The genus *Sminthopsis* represents one of the most successful and diverse extant groups of marsupials on the Australian continent. Radiation and speciation appear to have closely followed trends of increasing continental aridity and at least nineteen species are recognised (Mahoney & Ride, 1988) from habitats ranging from arid grasslands and deserts (Archer, 1981) to highland tropical rainforest (Van Dyck, 1985). In Papua New Guinea, where *Sminthopsis* is a recent invader, the genus is represented by two savannah-adapted species *S. virginiae* and *S. archeri*.

One of these, *S. virginiae*, was until recently, the only *Sminthopsis* recorded from the northern regions of the Northern Territory. However, on 25 October 1980, J.C. Wombey (CSIRO) collected a very young specimen of *Sminthopsis* (CM15587) in a pit trap set in open forest off the Arnhem Highway, west of Kapalga. The site was situated on an unnamed creek between the West Alligator River and Flying Fox Creek in Kakadu National Park, Northern Territory. The specimen was sent to John Calaby, (formerly of CSIRO, Canberra), who examined it and then sent it on to one of us (SVD) for comment. At the time it was concluded that this specimen represented a juvenile of *S. macroura*, and the specimen was referred to as *S. macroura* in the literature (Braithwaite, 1985; Brooker & Braithwaite, 1988). Later, having trapped an adult on the Mary River in November 1988, Wojnarski et al. (1989a) commented on the dubious nature of the earlier *S. macroura* references, and chose instead to favour a possible *S. butleri* determination for

the Kapalga and Mary River specimens. During the following 1989 wet season, CSIRO staff trapped a further nine dunnarts from Plumtree Creek, Gerowie, Mt Evelyn and Snake Plain, all within Stage III of Kakadu National Park. In April 1989, on the basis of foot and dental morphology, the Mary River specimen was taxonomically appraised as an undescribed species and in October that year Wojnarski et al. (1989b) noted the determination. Since then a small number of additional specimens has come to hand primarily through the Kakadu Stage III Fauna Survey. These specimens all confirm the early contention of Calaby that the Kapalga specimen represented a new species of dunnart. The species is described here as *S. bindi* and its close affinities with the *S. archeri*, *S. butleri*, *S. virginiae*, *S. douglasi* group are discussed.

METHODS

Terminology of cranial, external and dental morphology follows Archer (1976a, 1981). Tooth number follows Luckett (1993). Some extra measurements follow Van Dyck (1986). The HENNIG '86 V1.5 programme (James S. Farris, 1988) was used to formulate the most parsimonious hypothesis of relationship between *S. bindi* and other species of the genus; mhennig* and bb (branch breaker) options were used on unweighted branches using default coding. Seventy-nine characters were used in the analysis (Tables 2, 3). 17 pertained to the incisors, 5 to canines, 15 to premolars, 20 to molars, 8 to

cranium and 14 to external features. Polarity for many of these characters has been established in prior works such as Archer (1976b, 1981, 1982a, 1982b) and Kirsch & Archer (1982). The coded characters were treated as ordered. This analysis produced a single, well-resolved cladogram of dunnart relationships with a consistency index of 0.41. *Murexia longicaudata* and *Antechinus godmani* were used as outgroup species. A climate profile (Table 5) was generated by the BIOCLIM prediction system (see Nix & Switzer, 1991). Specimens mentioned here are lodged in the collections of the Queensland Museum (prefixed JM), Northern Territory Museum (U) and the Australian National Wildlife Collection, Division of Wildlife Research, Canberra (CM).

SYSTEMATICS

Sminthopsis bindi sp. nov., (Figs 1, 2; Tables 1, 4)

ETYMOLOGY

'Bindi' is the name for small dasyurids in the language of the Jawoyn people, traditional owners of the land from which most specimens have been recorded (Sandy Barruwei, Peter Jatbula and Nipper Cooper, as told to David Cooper).

TYPE LOCALITY

Eva Valley Station, Stage 3 Kakadu National Park, Northern Territory, 14°30'S, 132°45'E.

MATERIAL EXAMINED

HOLOTYPE: NTMU944, adult male, skull and dentaries, body in ethanol, 22 Feb 1991, J. Woinarski.

PARATYPES: A total of seven (Table 1).

DIAGNOSIS.

A small-sized species of *Sminthopsis* that differs from *S. murina*, *S. dolichura*, *S. griseoventer*, *S. gilberti*, *S. aitkeni*, *S. ooldea*, *S. granulipes*, *S. psumphophila*, *S. butleri*, *S. hirtipes*, *S. macroura*, *S. crassicaudata* and *S. youngsoni* in having the apical granules of the non-fused interdigital pads of the very narrow hindfeet large, oval and striate. Differs from *S. virginiae* in being much smaller [mean basicranial length (BL)=23.40mm (SD=0.70, N=5, R=22.95-24.40) vs BL=27.06 (SD=1.48, N=7, R=24.95-29.19), mean lower premolar row length (P₁₋₃)=3.00 (SD=0.19 N=5, R=2.88-3.30) vs P₁₋₃=3.83 (SD=0.16, N=7, R=3.67-4.11), mean hind foot width (HFW)=3.09 (SD=0.16, N=5, R=2.94-3.31) vs HFW=4.89 (SD=0.36, N=12, R=4.50-5.66)],

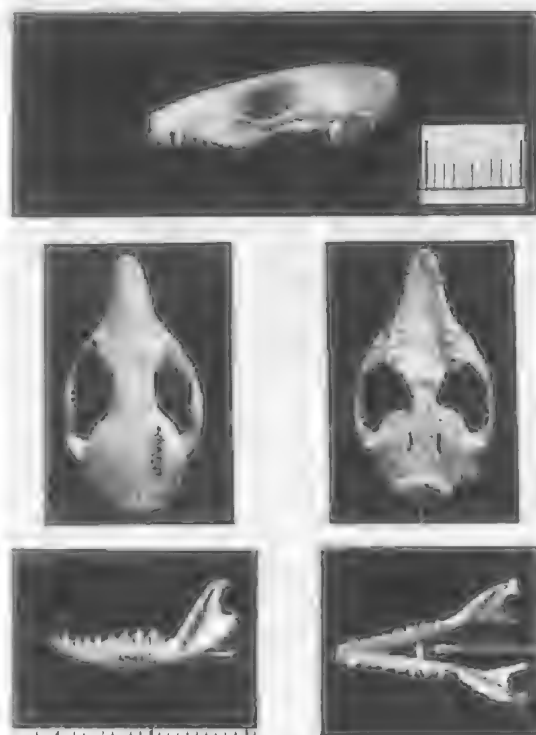


FIG. 1. *Sminthopsis bindi*, skull and dentaries of holotype, NTMU944. Scale in mm.

lacking rufous cheeks and having less well-developed entoconids. Differs from *S. longicaudata* in having a tail that is less than twice the nose-vent length. Differs from *S. douglasi* in being much smaller [mean BL=23.40 vs 28.90 (SD=3.11, R=26.7-31.10, N=2), mean P₁₋₃=3.00 vs 4.02 (SD=0.30, R=3.81-4.23, N=2), mean HFW=3.09 vs 5.30 (N=1)], lacking an incrassated tail, and having less well-developed entoconids. Differs from *S. leucopus* and *S. archeri* in possessing entoconids on M₁₋₃. Differs from *Antechinomys laniger* in lacking terminal brush on tail.

DESCRIPTION

This diminutive, broad-faced dunnart (Fig. 2) is characterised by sandy dorsal tonings, white belly, short-haired non-incrassated tail and distinctive eye-rings. There is little variation in the depth of tonings of specimens.

Holotype: *Pelage*. Colours (after Ridgway, 1912) for holotype are as follows; fur of mid-back (7mm long) with basal 4mm Slate Color, median 2.5mm Chamois, apical 0.5mm black. Back appears

TABLE 1. Paratypes.

| Reg. No. | Age | Sex | Locality | Collection date | Collector | Preservation |
|-----------|----------|--------|---|-----------------|--------------|------------------------------|
| NTMU716 | Adult | Male | El Sherana Plateau (Kakadu NP Stage III) 13°31'S 132°33'E | 1.8.90 | A. Fisher | Spirit body, skull extracted |
| NTMU943 | Juvenile | Male | Eva Valley 14°30'S 132°45'E | 2.2.91 | J. Woinarski | Spirit |
| NTMU945 | Juvenile | Male | Stuart Highway 12°51'S 131°08'E | 4.11.90 | R. Chatto | Spirit |
| NTMU946 | Adult | Male | Arnhem Highway 12°53'S 131°40'E | 21.10.90 | R. Chatto | Spirit |
| NTMU954 | Subadult | Female | Roper Valley Station 14°55'S 133°54'E | 27.5.91 | J. Woinarski | Spirit |
| CM15587 | Juvenile | Male | West of Kapalga 12°46'S 132°15'E | 25.10.80 | J.C. Wombey | Puppet skin, skull extracted |
| QMJM10121 | Adult | Male | James Mine. Adit Mt Todd area 14°07'S 132°08'E | 8.12.89 | M. Schulz | Spirit |

overall Citrine-Drab. Medially-thickened Fuscous Black spines (guard hairs) interspersed thinly through the fur 8 mm long on the rump and reduced to 5.5mm where they terminate at the crown of the head. Fur on and below the shoulders, thighs, flanks and chin lacks black tips or coarse guard hairs and these areas and the belly appear Dark Olive-Buff.

Holotype lacks distinct head-stripe, but light areas immediately above each eye-ring leave the impression of a dark head "patch". A distinct eye-ring results firstly from an intense darkening of the eyelid skin (similar in intensity to the dark pigmentation of the scrotal skin) and secondly from the dark hairs which surround the eye. A narrow band of short, black, eyelash-hairs completely encircles the eye. Fur immediately under the eye is off-white (Pale Olive-Buff) giving the impression of white cheeks. The soft ventral fur (4.5mm long on belly and 4mm long on inter-ranal region) is white and is interspersed by white medially-thickened spines up to 7 mm long. Belly is overall white. Forefeet thinly covered with short white hairs. Hindfeet more thickly covered with short white hairs. Tail weakly bicoloured with hairs averaging 1.0mm along its length and increasing to 2.2mm at its tip. Dorsally, hairs of tail uniform Pale Olive-Buff with Buffy Brown to Fuscous Black tips. Ventrally, black tips lost completely and hairs are Pale

Olive-Buff. However, the dark pigmentation of the tail scales gives the overall impression of a tail coloured Buffy Brown dorsally and Vinaceous-Buff ventrally.

Vibrissae. Approximately 25 mystacial vibrissae occur on each side and are up to 21mm long. More dorsal mystacial vibrissae are coloured Fuscous Black while those more ventral are colourless; supraorbital vibrissae (Fuscous Black) number 2 (right) and 1 (left); genals (Fuscous Black and colourless) number 10(right) and

9 (left); ulna-carpals (colourless) number 2 (left) and 2 (right); submentals (colourless) number 4.

Tail. Tail longer than nose-vent length. Thin and tapers toward tip.

Hindfoot. Very narrow. Interdigital pads separate. Apical granule enlarged, elongate and striate. Small hallucal granules present. No metatarsal granules present. Hair on foot covers heel and extends diagonally across foot. Terminal pads of digits also striate (Fig. 3).

Ears. Ears large with curled external edge on supratragus. Fawn hairs on posteroventral and ventral margins of pinnae.

Dentition. (Figs 1, 4). Upper incisors: I^1 narrow, peg-like, non-procumbent and relatively uncurved, taller-crowned than all upper incisors and separated by diastema from I^2 . Left and right I^1 worn and very widely separated. For I^{2-4} overall crown size $I^4 = I^3 > I^2$. I^2 and I^3 have very weak buccal cingula. There is no lack of differentiation between root and crown. I^4 carries a very weak anterior and posterior cusp. Roots of I^4 narrow.

Upper canines: C^1 slender, short and caniniform with indistinct boundary between root and crown. No buccal cingulum, no lingual cingulum. Minute anterior cusp present as well as minute posterior cusp.

Upper premolars: Minute gaps between C^1 and P^1 , P^1 and P^2 , P^2 and P^3 . All upper premolars carry



FIG. 2. Adult female and young *Sminthopsis bindi*. (Photo : Martin Armstrong).

weak buccal cingula. P^2 and P^3 carry weak lingual cingula. Crown height of $P^1 < P^2 < P^3$. Minute but clearly-defined anterior and posterior cingular cusps on P^1 , P^2 and P^3 . P^3 exhibits a slight postero-lingual lobe.

Upper molars: Posterior tip of P^3 near parasylar corner of M^1 but lingual to and below stylar cusp A. Anterior cingulum of M^1 below stylar cusp B short, broad and complete. Stylar cusp B and paracone relatively unworn and no protoconule present at base of paracone apex. Small bulge of enamel on face of anterior protocrista. Paracone on M^1 approximately one third height of metacone. Stylar cusps C and E not visible on either LM^1 or RM^1 . M^1 lacks posterior cingulum.

In M^2 very narrow incomplete anterior cingulum, which contacts metastylar corner of M^1 , tapers quickly along base of paracrista and degenerates well labially to base of paracone apex. Protoconule absent. M^2 lacks stylar cusps A, C and E. Stylar cusp D spinous and narrow and there is no posterior cingulum.

In M^3 anterior cingulum greatly reduced and narrower than in M^2 , becomes indistinct after covering half the distance between stylar cusp B and base of paracone. No evidence of anterior

cingulum at base of paracone and no protoconule or enamel bulge. Stylar cusp D reduced to very small, blunt peak. Stylar cusp E a minute point, but stylar cusp C absent.

In left M^4 anterior cingulum narrow and terminates half way between stylar cusp B and base of paracone. Posterior cingulum is absent. Protocone reduced, short and relatively narrow. In occlusal view angle made between postprotocrista and lingual profile of enamel below metastylar corner close to 120° . Right M^4 deformed and amorphous posterior to paracrista.

Lower incisors: Crown height in first lower incisor greater than crown height in I_2 . I_1 and I_2 oval in anterolateral view and gouge-like in occlusal view. I_2 greater in crown height than I_3 . I_3 slightly premolariform in lateral view with small posterior cusp at base of crest which descends posteriorly from apex of primary cusp. Lower canine rests against this posterior cusp. In occlusal view, a small notch separates posterior cusp from posterolingual lobe and crown enamel of primary and posterior cusps folds noticeable lingually such that the crest of the two cusps bisects tooth longitudinally.

Lower canines: C_1 caniniform and characterised by forward, incisor-like projection and



FIG. 3. Left hindfoot of *Sminthopsis bindi* holotype, NTMU944.

minimal curvature from root to crown tip. It has weak buccal and stronger lingual cingula and a very small posterior cusp.

Lower premolars: P_1 close to C_1 . All premolars close but not touching. All weakly cingulated buccally and very weakly lingually. For crown height and length $P_3 > P_2 > P_1$. All premolars narrow and elongate. All possess posterior cusps, and minute anterior cusps. Bulk of each premolar

mass concentrated anteriorly to line drawn transversely through middle of the two premolar roots.

Lower molars (Fig.4): All molars narrow. M_1 talonid wider than trigonid and anterior cingulum very poorly developed. It terminates at posterior base of protoconid. No buccal cingulum. Low narrow paraconid appears in occlusal view as small blunt spur, lingual edge of which makes a

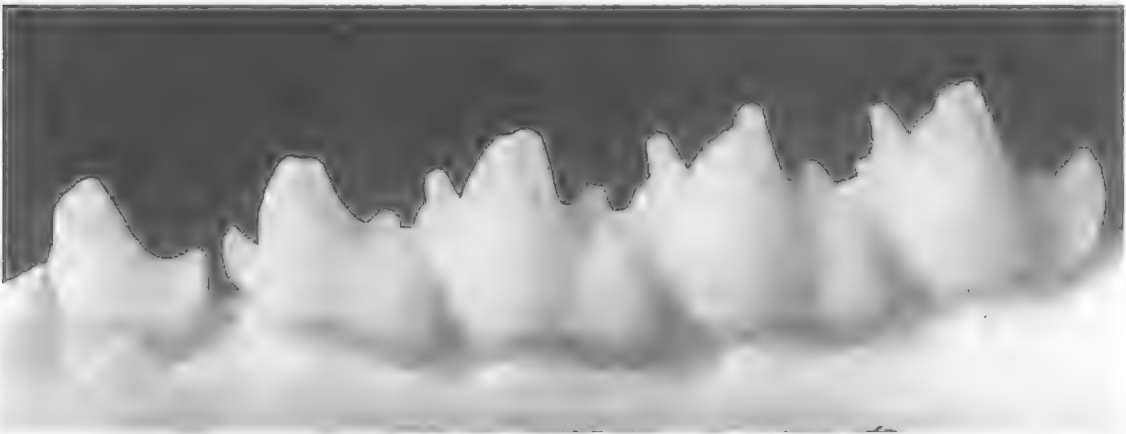


FIG. 4. Molar row of left dentary showing development of entoconids, holotype, NTMU944.

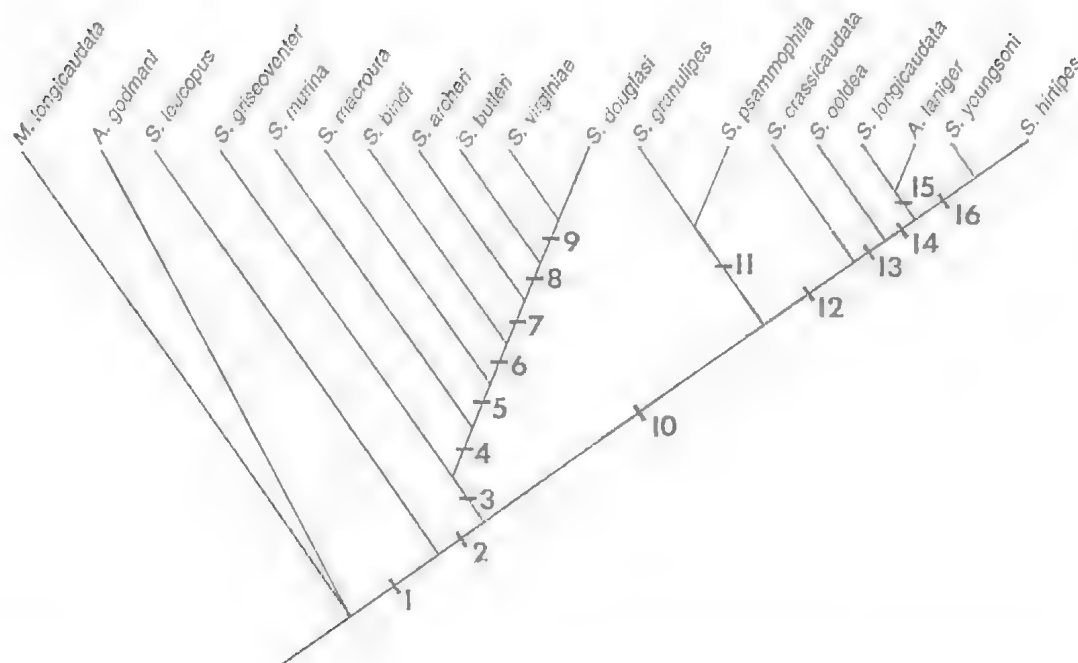


FIG. 5. The most parsimonious cladogram of 17 species of extant *Sminthopsis* (sensu Archer, 1982) when the outgroup contained *A. godmani* and *M. longicaudata*.

[Characters supporting the nodes in Fig. 5 are as follows (interpret character numbers from Table 2):

Node 1: non-homoplasious forward changes - 16(3), 19(1), 28(2), 36(2), 53(3), 54(1), 56(1), 62(1), 63(2), 79(2); homoplasious forward changes - 30(2) also at nodes 6, 9, 12, and in *M. longicaudata*, *A. laniger* and *S. hirtipes*, 32(4) also at nodes 8 and 13 and in *M. longicaudata*, *S. granulipes* and *A. laniger*, 70(1) also at nodes 2, 6, 9, 10, 11, 14, 16 and in *S. butleri*, *S. ooldea*, *A. laniger* and *S. hirtipes*.

Node 2: non-homoplasious forward changes - 58(1); homoplasious forward changes - 23(1) also in *A. godmani*, *S. archeri*, *S. douglasi*, *S. psammophila*, *S. ooldea*, *A. laniger* and *S. youngsoni*, 25(1) also at nodes 5, 13 and in *A. godmani*, *S. butleri*, *S. douglasi* and *S. longicaudata*, 42(1) also at node 15 and in *A. godmani*, *S. murina*, *S. granulipes*, *S. psammophila*, *S. ooldea*, 70(2) also at nodes 1, 6, 9, 10, 11, 14, 16 and in *S. butleri*, *S. ooldea*, *A. laniger* and *S. hirtipes*; non-homoplasious reversals - 1(0).

Node 3: homoplasious forward changes - 41(1) also at nodes 5, 11, 16 and in *S. psammophila*, 45(1) also at node 16 and in *S. archeri*, *S. virginiae* and *S. ooldea*, 58(2) also at nodes 2, 4, 5, 6 and in *S. butleri*, *S. virginiae*, *S. granulipes*, *S. psammophila*, *S. longicaudata*, *A. laniger* and *S. hirtipes*; homoplasious reversals - 5(0) also at nodes 8, 11 and in *M. longicaudata*, *A. godmani*, *S. douglasi*, *S. ooldea*, *A. laniger* and *S. hirtipes*.

Node 4: non-homoplasious forward changes - 58(3); homoplasious forward changes - 47(1) also in *S. ooldea*, 59(1) also at nodes 5, 14 and in *M. longicaudata*, *S. leucopus*, *S. macroura*, *S. butleri*, *S. longicaudata* and *S. hirtipes*.

Node 5: homoplasious forward changes - 4(2) also at nodes 11, 15 and in *M. longicaudata*, *S. murina*, *S. douglasi* and *S. granulipes*, 59(2) also at nodes 4 and 14 and in *M. longicaudata*, *S. leucopus*, *S. macroura*, *S. butleri*, *S. longicaudata* and *S. hirtipes*; homoplasious reversals - 2(0) also at node 9 and in *M. longicaudata*, *S. douglasi*, *S. granulipes*, *S. psammophila*, *S. crassicaudata*, *S. ooldea*, *S. hirtipes* and *S. youngsoni*, 25(0) also at nodes 2, 13 and in *A. godmani*, *S. butleri*, *S. douglasi* and *S. longicaudata*, 41(0) also at nodes 3, 11, 16 and in *S. psammophila*.

Node 6: homoplasious forward changes - 24(1) also in *S. youngsoni*, 30(3) also at node 1, 9, 12, and in *M. longicaudata*, *A. laniger* and *S. hirtipes*, 52(1) also at nodes 9, 12, 16 and in *S. psammophila*, 58(5) also at nodes 2, 4, 5, and in *S. butleri*, *S. virginiae*, *S. granulipes*, *S. psammophila*, *S. longicaudata*, *A. laniger* and *S. hirtipes*; homoplasious reversals - 8(0) also at nodes 11, 13 and in *S. virginiae*, *S. granulipes*, *S. longicaudata*, and *S. youngsoni*, 70(1) also at nodes 1, 2, 9, 10, 11, 14, 16 and in *S. butleri*, *S. ooldea*, *A. laniger* and *S. hirtipes*.

Node 7: homoplasious reversals - 19(0) also occurs at nodes 11, 15 and in *S. griseoventer* and *S. ooldea*, 43(0) also occurs at node 12 and in *M. longicaudata*, *S. murina*, *S. douglasi*, *S. ooldea*, and *S. longicaudata*.

Node 8: homoplasious forward changes - 5(1) also at nodes 3, 8, 11 and in *M. longicaudata*, *A. godmani*, *S. douglasi*, *S. ooldea*, *A. laniger* and *S. hirtipes*, 59(4) also at nodes 4, 5, 14 and in *M. longicaudata*, *S. leucopus*, *S. macroura*, *S. butleri*, *S. longicaudata* and *S. hirtipes*, homoplasious reversals - 32(3) also at nodes 1, 8, 13 and in *M. longicaudata*, *S. granulipes* and *A. laniger*, 79(1) also at node 1 and in *M. longicaudata*, *S. psammophila*, *S. ooldea*, *A. laniger* and *S. youngsoni*; non-homoplasious reversals 16(2) also at nodes 1 and 15 and in *M. longicaudata*, *S. douglasi* and *S. ooldea*.

Node 9: non homoplasious forward change - 21(2) also at node 10 and in *M. longicaudata*, *S. ooldea*, and *S. youngsoni*; homoplasious forward changes - 11(1) also at node 2 and in *S. douglasi*, *S. granulipes*, and *S. hirtipes*, 21(1) also at node 5, and in *M. longicaudata*, *S. douglasi*, *S. granulipes*, *S. psammophila*, *S. crassicaudata*, *S. ooldea*, *S. hirtipes* and *S. youngsoni*, 91(1) also in *S. douglasi*, and *S. psammophila*, homoplasious reversals - 30(2) also at nodes 1, 6 and 12 and in *M. longicaudata*, *A. laniger* and *S. hirtipes*, 52(1) also at nodes 6, 12, 16 and in *S. psammophila*, 54(0) also at nodes 1, 13 and in *S. leucopus*, *S. murina*, *S. archeri*, *S. butleri* and *S. crassicaudata*, 70(0) also at nodes 1, 2, 6, 10, 11, 14, 16 and in *S. butleri*, *S. ooldea*, *A. laniger* and *S. hirtipes*.

Node 10: non-homoplasious forward change - 70(1) also at nodes 1, 2, 6, 9, 11, 14, 16 and in *S. butleri*, *S. ooldea*, *A. laniger* and *S. hirtipes*, homoplasious reversal - 21(0) also at node 9 and in *M. longicaudata*, *S. ooldea*, and *S. youngsoni*.

Node 11: non-homoplasious forward change - 71(2), 96(2) and 70(4); homoplasious forward changes - 4(2) also at node 5 and in *M. longicaudata*, *S. murina*, *S. douglasi* and *S. granulipes*, 51(4) also at nodes 3, 8 and in *M. longicaudata*, *A. godmani*, *S. douglasi*, *S. ooldea*, *A. laniger* and *S. hirtipes*, 80(3) occurs also at nodes 6, 13 and in *S. virginiae*, *S. granulipes*, *S. longicaudata*, and *S. youngsoni*, 22(1) also at node 15 and in *M. longicaudata*, *S. granulipes* and *S. longicaudata*, 41(1) also at nodes 3, 5, 16 and in *S. psammophila*, homoplasious reversals - 18(0) also at node 15 and in *M. longicaudata*, *S. douglasi* and *S. hirtipes*, 19(0) also at nodes 1, 7, 15 and in *S. griseoventer* and *S. ooldea*, 35(1) also in *M. longicaudata* and *S. longicaudata*, 44(0) also in *M. longicaudata*, *S. macroura*, *S. bindi*, *S. douglasi*, *S. ooldea*, *A. laniger* and *S. youngsoni*.

Node 12: homoplasious forward changes - 20(1) also at node 15 and in *A. godmani*, *S. griseoventer*, *S. archeri* and *S. hirtipes*, 30(3) also at nodes 1, 6, 9 and in *M. longicaudata*, *A. laniger* and *S. hirtipes*, 52(1) also at nodes 6, 9, 16 and in *S. psammophila*, 68(1) also at node 15 and in *S. douglasi* and *S. granulipes*; homoplasious reversal - 43(0) also at node 7, and in *M. longicaudata*, *S. murina*, *S. douglasi*, *S. ooldea*, and *S. longicaudata*.

Node 13: homoplasious forward changes - 17(1) also at node 15 and in *A. godmani*, *S. griseoventer*, *S. bindi*, *S. archeri*, *S. douglasi* and *S. youngsoni*, 32(5) also at nodes 1 and 8 and in *M. longicaudata*, *S. granulipes* and *A. laniger*, 54(2) also at nodes 1 and 9 and in *S. leucopus*, *S. murina*, *S. archeri*, *S. butleri* and *S. crassicaudata*; homoplasious reversals - 8(0) also at nodes 6 and 11 and in *S. virginiae*, *S. granulipes*, *S. longicaudata*, and *S. youngsoni*, 25(0) also at nodes 2, 5, 13 and in *A. godmani*, *S. butleri*, *S. douglasi* and *S. longicaudata*.

Node 14: non-homoplasious forward change - 70(5); homoplasious forward changes 58(1) also at node 5 and in *M. longicaudata*, *S. leucopus*, *S. macroura*, *S. butleri*, *S. longicaudata* and *S. hirtipes*, 64(2) also at node 15 and in *M. longicaudata* and *S. psammophila*.

Node 15: non-homoplasious forward changes - 17(3), 18(3), 19(4), 20(2), 64(2), 65(2); homoplasious forward changes - 4(2) also at nodes 5, 11 and in *M. longicaudata*, *S. murina*, *S. douglasi* and *S. granulipes*, 16(4) also at nodes 1 and 8 and in *M. longicaudata*, *S. douglasi*, *S. granulipes* and *S. ooldea*, 22(1) also at node 11 and in *M. longicaudata*, *S. granulipes* and *S. longicaudata*, 69(1) also in *S. psammophila*; homoplasious reversals - 42(0) also at node 2 and in *A. godmani*, *S. murina*, *S. granulipes*, *S. psammophila*, *S. ooldea*, 65(0) also in *M. longicaudata*, *S. granulipes*, *S. psammophila*, *S. crassicaudata* and *S. youngsoni*, 68(0) also at node 12 and in *S. douglasi* and *S. granulipes*.

Node 16: non-homoplasious forward change - 70(7) also at nodes 1, 2, 6, 9, 10, 11, 14, and in *S. butleri*, *S. ooldea*, *A. laniger* and *S. hirtipes*; homoplasious forward changes - 41(2) also at nodes 3, 5, 11, and in *S. psammophila*, 45(1) also in *S. archeri* and *S. ooldea*; homoplasious reversals - 52(0) also at nodes 6, 9, and 12 and in *S. psammophila*.

slight swelling on endoloph of M_1 . Metacristid roughly oblique to long axis of dentary while hypocristid perpendicular. Cristid obliqua very short and extends from hypoconid to posterior wall of trigonid intersecting trigonid at point directly below tip of protoconid. Hypocristid terminates two-thirds way between hypoconid and metastylid. Small entoconid. From base of metaconid posteriorly, talonid endoloph takes a more lingual orientation under the influence of the entoconid.

In M_2 , trigonid slightly narrower than talonid. Anterior cingulum poorly developed and terminating lingually in weak parastylid notch into which hypoconulid of M_1 is tucked. No buccal cingulum. Narrow, weak posterior cingulum extends from hypoconulid to posterior base of hypoconid. Well-developed paraconid is smallest trigonid cusp. Metastylid minute, entoconid small but moderately well developed. Cristid obliqua extends from hypoconulid to posterior wall of trigonid, intersecting trigonid at point slightly lingual to longitudinal vertical midline

TABLE 2. Character states (defined in derived state) used to resolve the affinities of *S. bindi*. Data used are a small subset of data including representatives from the following genera: *Marmosa*, *Philander*, *Antechinus*, *Phascogale*, *Myiictis*, *Dasyurus*, *Pseudantechinus*, *Parantechinus*, *Sarcophilus*, *Peroryctes*, *Isodon* and *Myrmecobius*. However the cladogram (Fig. 5) was based only upon taxa in Table 3. Character states are taken unchanged from those of the full data set, hence there are some discontinuities.

UPPER INCISORS

1. Incisors procumbent; 0, not procumbent; 1, slightly procumbent; 2, more than 1; 3, more than 2; 4, procumbent.
2. I¹ crown relatively bulky with cingulum low; 0, crown of I¹ a thin spur; 1, more bulky than 0; 2, bulkier than 1; 3, bulkier than 2; 4, bulkier than 3; 5, bulkier than 4; 6, I¹ crown heavy.
3. I¹ laterally compressed, elongate; 0, I¹ needle or peg-like; 1, more compressed than 0; 2, more compressed than 1; 3, more compressed than 2; 4, I¹ spade-like.
4. R and L I¹ separated by diastema; 0, touching; 1, narrowly spaced; 2, wider than 1; 3, wider than 2; 4, widely spaced.
5. I¹ non-needle-like; 0, I¹ needle-like; 1, less needle-like than 0; 2, less needle-like than 1; 3, less needle-like than 2; 4, less needle-like than 3; 5, less needle-like than 4; 6, less needle-like than 5; 7, I¹ spatulate or club-shaped.
6. I¹ and I² juxtaposed; 0, I¹ and I² widely spaced; 1, spacing less than 0; 2, spacing less than 1; 3, spacing less than 2; 4, spacing less than 3; 5, I¹ and I² crushed.
7. I¹⁻⁴ crowns broader than roots; 0, crown-root width equal; 1, crown slightly broader; 2, broader than 1; 3, broader than 2; 4, broader than 3; 5, crown much broader than root.
8. I¹ lensate, elongate; 0, I¹ peg-like; 1, more elongate than 0; 2, more than 1; 3, more than 2; 4, more than 3; 5, I¹ lensate.
9. I¹⁻⁴ crowns broad (occlusal) and cusps folded lingually; 0, crowns narrow and cusps unfolded; 1, crowns broader and slightly folded; 2, more than 1; 3, more than 2; 4, crowns broad and folded.
10. I¹ > I² > I³; 0, I¹ > I³ > I²; 1, I¹ = I³ > I²; 2, I² > I¹ > I³; 3, I² > I³ > I¹; 4, I² > I¹ > I³.
11. I¹ cingulated; 0, no cingulation; 1, slight cingulation; 2, more than 1; 3, more than 2; 4, I¹ heavily cingulated.
12. I¹ with posterior cusp; 0, no posterior cusp; 1, posterior cusp present.
13. Total upper incisors = 8; 0, 10; 1, 8.
14. I¹ greatly enlarged; 0, no; 1, yes.
15. I¹ lower than I²; 0, higher; 1, lower.

UPPER CANINES

16. C¹ short; 0, C¹ very long; 1, shorter than 0; 2, shorter than 1; 3, shorter than 2; 4, C¹ short.
17. C¹ root and crown clearly differentiated; 0, no differentiation; 1, differentiated; 2, more than 1; 3, more than 2; 4, more than 3.
18. C¹ bulky, non needle-like; 0, C¹ needle-like; 1, less than 0; 2, less than 1; 3, less than 2; 4, C¹ cone-shaped.
19. C¹ non-caniniform; 0, C¹ caniniform; 1, less than 0; 2, less than 1; 3, less than 2; 4, C¹ premolariform.
20. C¹ with posterior cusp; 0, cusp absent; 1, small cusp present; 2, cusp larger than 1.

UPPER PREMOLARS

21. P¹ circular in occlusal; 0, P¹ elongate; 1, more rounded than 0; 2, more rounded than 1; 3, more rounded than 2.
22. P¹ extremely lensate; 0, P¹ moderately narrow; 1, more elongate than 0; 2, more elongate than 1; 3, more elongate than 2; 4, P¹ very narrow and lensate.
23. P¹ and P² touching or crushed; 0, wide space between P¹ and P²; 1, small space between P¹ and P²; 2, P¹ and P² touch or crushed.

24. P¹ and P² with lingual lobing; 0, no lobing; 1, slight lobing; 2, pronounced lobing.
25. P¹ with large posterior cusp; 0, no cusp; 1, slight cusp; 2, pronounced cusp or P² absent.
26. P³ < P²; 0, no P² < P³; 1, yes.
27. P³ with postero-lingual cusp; 0, no; 1, yes.

UPPER MOLARS

28. M¹⁻³ narrow with incomplete anterior cingulum; 0, M¹⁻³ broad, cingulum complete; 1, M¹⁻³ narrow, cingulum incomplete or nearly so; 2, M¹⁻³ narrow, cingulum incomplete, molars very narrow; 3, molars greatly reduced.
29. M¹⁻³ equal to or shorter than M²; 0, no; 1, yes.
30. M¹⁻³ protocone width greatly reduced; 0, Protocone broad; 1, protocone narrower than 0; 2, narrower than 1; 3, narrower than 2; 4, narrower than 3; 5, protocone absent.
31. M¹ stylar cusp B greatly reduced; 0, no reduction; 1, reduced; 2, greatly reduced.
32. M¹ protocone reduced; 0, protocone large; 1, protocone slightly reduced; 2, reduction greater than 1; 3, reduction greater than 2; 4, reduction greater than 3; 5, reduction greater than 4; 6, reduction greater than 5; 7, reduction greater than 6; 8, protocone absent.
33. M¹ preparacrista orients transversely to long axis of skull; 0, orientation perpendicular to longitudinal; 1, slightly transverse; 2, transverse.
34. M¹⁻³ stylar cusp D very large; 0, stylar cusp D absent; 1, larger than 0; 2, larger than 1; 3, stylar cusp D very large.
35. M², M³ ectoloph greatly indented; 0, no; 1, slight indent; 2, more than 1; 3, greatly indented.
36. M¹ metacone loss; 0, metacone large; 1, metacone more reduced than 0; 2, more than 1; 3, more than 2; 4, metacone lost.
37. M² posterior cingulum absent; 0, present; 1, absent.
38. M², M³ metaconule greatly developed; 0, no; 1, slight development; 2, greatly developed.
39. M¹ paracone and stylar cusp B fused; 0, no, widely separated; 1, approximated; 2, greater approximation than 1; 3, fused.
40. Stylar cusp D on M³ heavily infolded; 0, near perpendicular with ectoloph; 1, slightly infolded; 2, heavily infolded; 3, merging with metacone.

LOWER INCISORS

41. I₁, I₂ prostrate; 0, I₁, I₂ almost perpendicular to dentary axis; 1, more prostrate than 0; 2, more prostrate than 1; 3, I₁, I₂ almost horizontal.
42. I₁ heel narrower than I₁ heel; 0, I₁ heel wider than heel of I₁; 1, heels equal width; 2, I₁ heel slightly narrower than heel of I₁; 3, narrower than 2; 4, narrower than 3.

LOWER PREMOLARS

43. P₃ < P₂; 0, P₃ > P₂; 1, P₃ ≤ P₂; 2, P₃ << P₂.
44. Lower premolars crushed; 0, premolars widely spaced; 1, nearly touching; 2, slightly crushed; 3, more than 2; 4, more than 3.
45. P₁, P₂ in contact; 0, widely spaced; 1, just contacting; 2, crushed.

46. P₃ broad or oriented transversely: 0, P₃ longitudinal to dentary axis; 1, P₃ broad; 2, P₃ transverse to dentary axis.
 47. P₁₋₃ circular in occlusal view: 0, premolars elongate view; 1, premolars oval; 2, premolars round.
 48. P₂, P₃ lenticular: 0, elongate; 1, narrower than 0; 2, narrower than 1; 3, lenticular.
 49. P₁, P₂ with posterior lobing: 0, no lobing; 1, slight lobing; 2, heavily lobed.
 50. P₃ single-rooted or absent: 0, neither; 1, yes, one or both.

LOWER MOLARS

51. M₁ paraconid poorly developed: 0, paraconid well developed; 1, paraconid more reduced than 0; 2, paraconid more reduced than 1.
 52. M₃ talonid narrower than trigonid: 0, no; 1, yes.
 53. M₄ talonid with reduced cusp number: 0, 3 cusps, well developed; 1, 3 cusps, poorly developed; 2, 2 cusps; 3, 1 cusp; 4, loss of talonid.
 54. M₂ entoconid reduced: 0, entoconid tall; 1, reduced; 2, absent.
 55. M₁ paraconid absent: 0, present; 1, absent.
 56. M₁₋₃ metaeistids and hypoeistids perpendicular to long axis of dentary: 0, transverse; 1, perpendicular.
 57. M₂, M₃ hypoconid coalesced with entoconid: 0, no; 1, yes.

CRANIAL FEATURES

58. Skull brachycephalic (ratio lachrymal breadth to length 1-lachrymal canal): 0, elongate; 1, less elongate than 0; 2, less elongate than 1; 3, less elongate than 2; 4, less elongate than 3; 5, less elongate than 4; 6, less elongate than 5; 7, skull brachycephalic.
 59. Skull brachycephalic (ratio zygomatic width to basicranial length): 0, elongate (<0.5690); 1, less elongate than 0 ($0.5691-0.5890$); 2, less elongate than 1 ($0.5897-0.6054$); 3, less elongate than 2 ($0.6055-0.6300$); 4, brachycephalic (>0.6300).
 60. Nasals non-fluted: 0, fluted; 1, less fluted than 0; 2, less fluted than 1; 3, flat.
 61. Skull flat not domed: 0, domed; 1, less than 0; 2, flat or concave.

62. Squamosal-frontal contact: 0, no; 1, yes.
 63. Maxillary vacuities present: 0, absent; 1, present; 2, very large or with palatine vacuities.
 64. Alisphenoid tympanic wing greatly expanded: 0, small expansion; 1, slightly inflated; 2, more inflated than 1; 3, greatly expanded.
 65. Periotic wing of alisphenoid mastoid greatly expanded: 0, slight expansion; 1, inflated; 2, greatly expanded.

EXTERNAL FEATURES

66. Supratragus folded: 0, simple; 1, folded.
 67. Tail short: 0, longer than head-body; 1, equal to head-body; 2, shorter than head-body.
 68. Tail incassated: 0, no, tail thin; 1, yes or capacity to fatten.
 69. Tail extremely long: 0, no; 1, yes.
 70. Hind foot interdigital pads: 0, large apical granules strongly striated; 1, large apical granules weakly striated; 2, large apical granules clear; 3, small apical granules; 4, no enlarged apical granules; 5, coalesced interdigitals, striated apical granules; 6, coalesced interdigitals, unstriated apical granules; 7, coalesced interdigitals, small apical granules and short hair cover; 8, coalesced interdigitals, small apical granules and long hair cover.
 71. Loss of hallux: 0, no; 1, yes.
 72. Hind foot heavily padded and striated post-hallucal granule: 0, no; 1, moderately; 2, yes.
 73. Claws very long: 0, no; 1, yes.
 74. Body striped: 0, no; 1, yes.
 75. Hind feet syndactylous: 0, no; 1, yes.
 76. Backward-opening pouch: 0, no; 1, yes.
 77. Tail with terminal brush: 0, no; 1, yes.
 78. Body size very large: 0, small; 1, medium; 2, large; 3, very large.
 79. Body size very small: 0, medium; 1, smaller than 0; 2, smaller than 1; 3, very small.

drawn through tip of protoconid but well buccal to metaeistid fissure. Hypoeistid extends from slightly anterior and buccal to hypoconulid, to tip of hypoconid. From base of metaconid moving posteriorly, the endoloph takes a lingual orientation, then veers buccally to follow the line of the dentary until the base of the hypoconulid.

In M₃, trigonid wider than talonid. Prominent parastylid wraps around hypoconulid of M₃; a strong anterior cingulum on M₃. Posterior cingulum as in M₂ but more developed. Reduced cristid obliqua intersects trigonid at point well lingual to longitudinal vertical midline drawn through tip of protoconid, but slightly buccal to metaeistid fissure. Entoconid on M₃ as in M₂ but less well developed. Endoloph on talonid of M₃ follows line of dentary axis. Rest of M₃ morphology as in M₂.

In M₄ trigonid much wider than talonid. Anterior cingulum stronger than in M₂. Posterior

cingulum absent. Of three main trigonid cusps, metaconid slightly taller than paraconid but both are dwarfed by protoconid. Hypoconid of M₄ talonid similar in size to M₃. Cristid obliqua forms low crest between hypoconid and base of metaeistid, which intersects trigonid at point well lingual to metaeistid fissure. Talonid crown enamel below cristid obliqua is reduced, resulting in talonid appearing (in occlusal view) as narrow oblique spur jutting off trigonid wall. Entoconid remnant visible.

Skull (Fig. 1). *Smintropsis bindi* is one of the 'broad-faced' dunnarts (others include *S. virginiae*, *S. butleri*, *S. archeri*, *S. douglasi*) which have a deep rostrum and broad zygomata giving the skull a brachycephalic appearance. Sagittal and nuchal crests poorly developed. Rostrum has longitudinal depression running along nasal sutures. Left and right alisphenoid tympanic wings of auditory bullae well developed and widely

separated. The foramen pseudovalve large, open and not bisected by a bridge of alisphenoid. Eustachean canal opening large. Internal jugular canal foramina large; canals raised and prominent. Posterior lacerate foramina large and exposed, as are entocrotid foramina. Premaxillary vacuity extends from level of I^2 root back to level of posterior edge of C^1 root. Small maxillary vacuities extend from level of posterior root of P^3 back to level of protocone root of M^3 . Palatine vacuities extend from level of protocone root on M^3 .

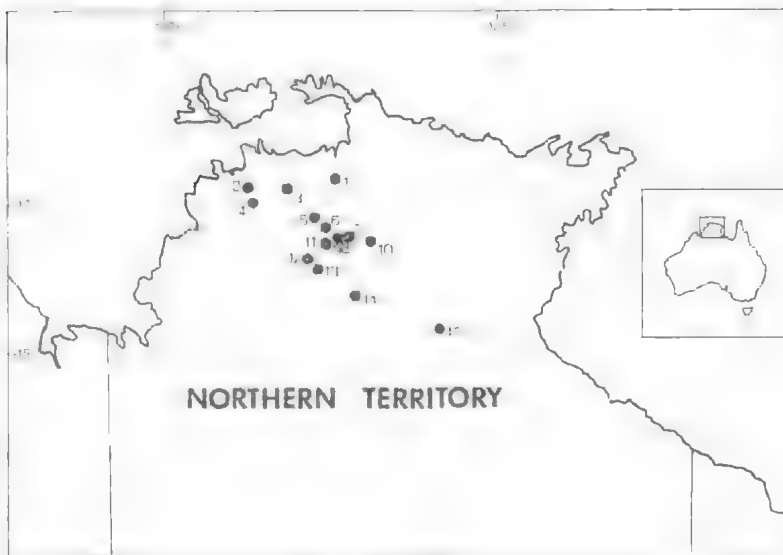


FIG. 6. Collection records for *Smynthopsis bindi* sorted by latitude. 1, West of Kapalga (12°46'S 132°15'E); 2, Stuart Hwy (12°51'S 131°08'E); 3, Arnhem Hwy (12°53'S 131°40'E); 4, Coomalie (13°01'S 131°07'E); 5, Snake Plain (13°12'S 132°16'E); 6, Gerowie (13°23'S 132°16'E); 7, Koolpin (13°30'S 132°35'E); 8, Plumtree Ck (13°31'S 132°27'E); 9, El Sharana (13°31'S 132°33'E); 10, Mt Evelyn (13°31'S 132°56'E); 11, Mary R (13°38'S 132°16'E); 12, Pine Ck (13°50'S 131°53'E); 13, Mt Todd (14°07'S 132°08'E); 14, Eva Valley (14°30'S 132°45'E); 15, Roper Valley (14°55'S 133°54'E).

VARIATION IN PARATYPES

In male CM15587 (juv) dp^3 is molariform, 3-rooted, with homologues of a protocone, paracone, metacone and styler cusp B. M^4 is unerupted. dp_3 is premolariform, 2-rooted, circular in occlusal view, and with buccal and lingual cingula. The entoconids on M_2 and M_3 are moderately well developed.

In male NTMU716 the upper canines are premolariform and ectoloph indentation in M^4 is pronounced. The apical granules on each interdental pad of the hind feet appear worn and calloused and striation is indistinct.

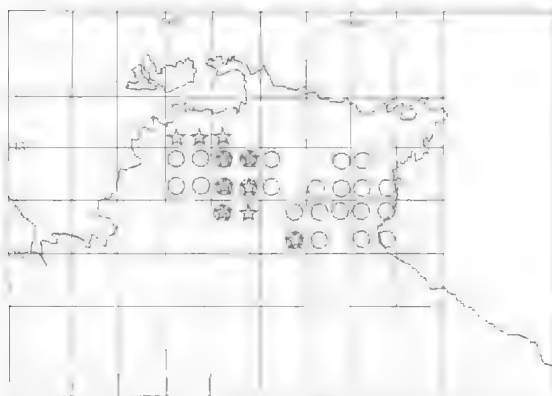


FIG. 7. Distribution of records of *Smynthopsis bindi* by 30' blocks (stars) along with BIOCLIM predictions (circles).

In adult male NTMU946 (a road-killed specimen) the head and body are badly squashed and the teeth show marked signs of decalcification.

The undeveloped pouch of subadult female NTMU954 shows 8 undeveloped nipples. The tail of this specimen is slightly thickened, giving the impression that it had the potential to incrassate.

The basicranium of adult male QMJM10121 is missing. Entoconids of the left dentary are low while those of the right are high and well developed. The right P_2 is abnormally developed with a high posterior cusp and matching abnormal development of the posterolingual lobe.

While hallucal granules were present on the hindfeet of the holotype and all paratypes, no metatarsal granules were recorded. Their presence in dried skin CM15587 was impossible to determine. Most specimens showed enlargement of one or two granules adjacent to either distal or proximal extremity of the prominent striated apical granule on each interdental pad.

TABLE 3. Distribution of characters states used to resolve the affinities of *S. bindi*. Characters are defined in the derived state.

| | | | | | | | | | | | | | | | | |
|---------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|------|
| <i>M. lo</i> | 10020 | 01100 | 00100 | 00000 | 01000 | 00000 | 02111 | 10000 | 00000 | 00000 | 10200 | 00010 | 00100 | 10000 | 01000 | 0010 |
| <i>A. go</i> | 11112 | 11101 | 10100 | 11101 | 10101 | 00101 | 03222 | 11011 | 01110 | 00000 | 00200 | 00003 | 20110 | 11000 | 10000 | 0001 |
| <i>S. ar</i> | 00020 | 01000 | 00100 | 31101 | 10010 | 00203 | 04122 | 31010 | 01010 | 01000 | 01320 | 10523 | 11210 | 11001 | 00000 | 0002 |
| <i>S. bi</i> | 00020 | 01000 | 00100 | 31110 | 10110 | 00203 | 04112 | 21010 | 01121 | 01010 | 01310 | 10523 | 11210 | 11001 | 00000 | 0002 |
| <i>S. bu</i> | 00021 | 01000 | 10100 | 20100 | 10111 | 00203 | 13132 | 21010 | 01011 | 01000 | 01320 | 10743 | 11210 | 11002 | 00000 | 0001 |
| <i>S. cr</i> | 00011 | 01100 | 01100 | 30111 | 00101 | 00203 | 04122 | 21010 | 01010 | 00000 | 01200 | 11103 | 21210 | 12103 | 00000 | 0002 |
| <i>S. do</i> | 23112 | 41021 | 00100 | 11200 | 20211 | 00212 | 03132 | 31010 | 01121 | 01010 | 00300 | 10543 | 11210 | 11100 | 00000 | 0001 |
| <i>S. gra</i> | 10034 | 12400 | 00101 | 00000 | 02101 | 00202 | 05121 | 21010 | 14100 | 00200 | 00310 | 10003 | 11210 | 12104 | 00000 | 0002 |
| <i>S. gri</i> | 01110 | 01100 | 00100 | 31121 | 10101 | 00202 | 04132 | 21010 | 11111 | 00000 | 00310 | 10203 | 11210 | 11002 | 00000 | 0002 |
| <i>S. hi</i> | 20010 | 01001 | 00100 | 31010 | 00100 | 00202 | 05222 | 21010 | 21011 | 00000 | 00320 | 10433 | 11221 | 11108 | 00000 | 0002 |
| <i>S. le</i> | 11011 | 01100 | 01100 | 30110 | 10000 | 00202 | 04122 | 21010 | 00110 | 00000 | 00320 | 10013 | 11210 | 11001 | 00000 | 0002 |
| <i>S. lo</i> | 01221 | 01301 | 00100 | 43342 | 02101 | 00203 | 05123 | 11010 | 00110 | 00100 | 01320 | 10023 | 01232 | 10015 | 02000 | 0002 |
| <i>S. ma</i> | 00020 | 01100 | 00100 | 30110 | 10100 | 00202 | 03122 | 21010 | 00121 | 01010 | 00310 | 10343 | 11210 | 11002 | 00000 | 0002 |
| <i>S. mu</i> | 01000 | 01100 | 00100 | 30010 | 10111 | 00202 | 04122 | 21010 | 12011 | 01000 | 00320 | 10313 | 11210 | 11002 | 00000 | 0002 |
| <i>S. oo</i> | 05014 | 01001 | 10100 | 41121 | 10200 | 00203 | 05122 | 31010 | 03121 | 01000 | 01320 | 10103 | 21210 | 11102 | 00000 | 0003 |
| <i>S. ps</i> | 04124 | 02310 | 10100 | 30000 | 01001 | 00202 | 14111 | 41022 | 20100 | 00200 | 01310 | 10203 | 01220 | 10014 | 00000 | 0001 |
| <i>S. vi</i> | 11021 | 01110 | 00100 | 20100 | 20110 | 00102 | 03112 | 21010 | 01010 | 01000 | 00200 | 10643 | 11210 | 11000 | 00000 | 0001 |
| <i>S. yo</i> | 02111 | 01100 | 00100 | 30111 | 10200 | 00203 | 05132 | 21010 | 21021 | 00000 | 00320 | 10113 | 11220 | 12107 | 00000 | 0003 |
| <i>S. la</i> | 01023 | 01000 | 00100 | 44342 | 01000 | 00202 | 04122 | 41010 | 00000 | 00000 | 01320 | 10513 | 11232 | 10016 | 10000 | 0101 |

Abbreviations: *M. lo*=*M. longicaudata*; *A. go*=*A. godmani*; *S. ar*=*S. urcheri*; *S. bi*=*S. bindi*; *S. bu*=*S. butleri*; *S. cr*=*S. crassicaudata*; *S. do*=*S. douglasi*; *S. gra*=*S. granulipes*; *S. gri*=*S. griseoventer*; *S. hi*=*S. hirtipes*; *S. le*=*S. leucopus*; *S. lo*=*S. longicaudata*; *S. ma*=*S. macroura*; *S. mu*=*S. murina*; *S. oo*=*S. ooldea*; *S. ps*=*S. psammophila*; *S. vi*=*S. virginiae*; *S. yo*=*S. youngsoni*; *S. la*=*S. (A.) laniger*.

REPRODUCTION

Paratypes CM15587 (collected 25 Oct 1980), NTMU943 (22 Feb 1991) and NTMU945 (4 Nov 1990) were probably newly weaned juveniles. U954 had 8 minute non-lactating nipples in a poorly developed pouch lined with long white hairs. No other substantial information is available for the species.

DISTRIBUTION

All known records are from the Top End of the Northern Territory (Fig. 6), with more than half being from the c.7000km² Stage III of Kakadu National Park. The distribution of records by 30' blocks is shown in Fig. 7 along with that predicted by BIOCLIM based on sixteen climatic parameters (Table 5). The species is predicted to occur in much of eastern and southern Arnhem Land, areas which have been subjected to remarkably little wildlife survey to date.

HABITAT

S. bindi has been recorded mainly from stony hills with woodland dominated by *Eucalyptus dichromophloia*, *E. tintinnans* (formerly *E. alba* in part), *E. rectiflora*, and *E. foelschewna*. In the Kakadu

Stage III area, *Sminthopsis bindi* is closely associated with gravel or stony substrates on rolling foothills and supporting woodland dominated usually by the partly deciduous *E. dichromophloia* and *E. tintinnans* (Woinarski, 1992) (Fig. 8). These substrate and topographic associations are consistent for most records beyond Kakadu, how-



FIG. 8. Northern Territory distribution of *Eucalyptus tintinnans*/*E. dichromophloia* woodland (solid) and *E. dichromophloia* woodlands (hatched).

TABLE 4. Measurements for holotype (H) and paratypes of *Sminthopsis bindi*. Some abbreviations are as follows: BL basicranial length; ZW zygomatic width; IO interorbital width (measured dorsally); R-LC¹ width of rostrum outside right and left upper canines; R-LM¹s width of skull from outside right and left upper first molars; R-LM¹m width of skull between right and left upper first molars; HB head-body length (tip of nose to cloaca); TV tail-vent length; HF_(su) hind-foot length; E_(n) ear length; Wt weight in g. * measurement taken from spirit specimen.

| Reg. No. | Age/ Sex | BL | ZW | IO | R-L C | R-L M2s | R-L M2m | I ¹ M ¹ | P1 ³ | M1 ⁴ | I ₁ - M ₁ | I ₁ - cond | P1-3 | M1-4 | HB | TV | HF | E | Wt | |
|----------|----------|---|------|-----|-------|---------|---------|-------------------------------|-----------------|-----------------|---------------------------------|-----------------------|------|------|-----|------|-------|-------|-------|----|
| U944 (H) | AM | 24.4 | 14.7 | 4.1 | 4.3 | 9.4 | 6.8 | 13.1 | 3.5 | 5.5 | 11.3 | 19.9 | 3.3 | 6.0 | 74* | 105 | 16.7 | 17.3* | | |
| U716 | AM | 22.7 | 13.5 | 3.9 | 4.3 | 9.1 | 6.9 | 12.4 | 3.4 | 5.6 | 10.9 | 17.8 | 2.9 | 6.2 | 79 | 99 | 15.3* | 18.2* | 14 | |
| JM 10121 | AM | Cranial fragments and hindquarters only, found at Ghost Bat Roost | | | | | | | | | | | | | | 103* | 16.6* | | | |
| U946 | AM | Squashed body and skull | | | | | | | | | | | | | | 90 | 84 | 16.4* | 19.6* | 12 |
| U954 | SAP | | | | | | | | | | | | | | 66* | 81* | 15.5* | 15.6* | | |
| CM 15587 | JM | 19.2 | 11.8 | 3.9 | 3.8 | 8.0 | 6.2 | | | | | | | | 64 | 70 | 14.2 | 13.6 | 6 | |
| U943 | JM | | | | | | | | | | | | | | 65 | 68* | 14.7* | 13.8* | | |

ever vegetation at the Roper River Valley site was predominantly *Acacia* thicket.

PHYLOGENETIC ANALYSIS

The distribution of character states for 79 characters (Table 2) among *Antechinus godmani*, *Murexia longicaudata*, *Antechinomys luniger* and 16 extant species of *Sminthopsis* is listed in Table 3. The phylogenetic analysis associated with this description was aimed primarily at evaluating the affinities of *S. bindi* with the *S. macroura* group (*S. macroura*, *S. butleri*, *S. virginiae*, *S. douglasi*, *S. hirtipes*, Archer, 1981; to which *S. archeri* was more recently added, Van Dyck, 1986). However, it is possible to suggest some of the broader relationships within the genus. When *A. godmani* and *M. longicaudata* comprised the outgroup, this analysis produced a single, well-resolved cladogram of dunnart relationships with 351 steps and a consistency index of 0.41 (Fig. 5). If a hypothetical ancestor exhibiting the presumed plesiomorphic states for all 79 characters was included in the analysis, one tree (366 steps, ci 0.42) of identical topology was resolved.

These analyses resolved the 17 tested species into 4 clades: 1, the broad *S. crassicaudata* clade comprised of sub-clades (a) *S. crassicaudata*, (b) *S. ooldea*, (c) *S. longicaudata* and *S. (Antechinomys) luniger*, (d) *S. hirtipes* and *S. youngsoni*; 2, The *S. psammophila* clade containing *S. psammophila* and *S. granulipes*; 3, The broad *S. macroura* clade comprised of sub-clades (a) *S. griseoventer*, (b) *S. murina*, (c) *S. macroura*, and (d) *S. bindi*, *S. butleri*, *S. virginiae*, *S.*

douglasi and *S. archeri* (all from tropical northern Australia); 4, the *S. leucopus* clade containing *S. leucopus* alone. They supported the sister group relationships proposed by Archer (1981) for *S. virginiae* with *S. douglasi* and *S. psammophila* with *S. granulipes*. However, the analysis did not support a hypothesis of sister species relationship between *S. hirtipes* and *S. butleri*; *S. crassicaudata* and *S. luniger*; or a close relationship between his *S. longicaudata* and the *S. ooldea*, *S. murina*, *S. leucopus* clade. While in the present analysis, resolution of *Sminthopsis* cladograms

TABLE 5. Climatic envelope (16 parameters) from locations of capture for *Sminthopsis bindi*.

| | Mean | S.D. |
|------------------------------------|------|------|
| Annual mean temperature °C | 27.0 | 0.4 |
| Minimum temp. (coolest month) °C | 14.3 | 1.4 |
| Maximum temp. (warmest month) °C | 36.7 | 0.6 |
| Annual temp. range °C | 22.3 | 1.9 |
| Mean temp. (coolest quarter) °C | 23.3 | 0.9 |
| Mean temp. (warmest quarter) °C | 29.8 | 0.3 |
| Mean temp. (wettest quarter) °C | 28.5 | 0.3 |
| Mean temp. (driest quarter) °C | 23.4 | 0.9 |
| Annual mean precipitation mm | 1240 | 163 |
| Precipitation (wettest month) mm | 282 | 32 |
| Precipitation (driest month) mm | 1 | 0 |
| CV (monthly precipitation) | 115 | 1.8 |
| Precipitation (wettest quarter) mm | 790 | 97 |
| Precipitation (warmest quarter) mm | 421 | 75 |
| Precipitation (driest quarter) mm | 6 | 1 |
| Precipitation (coolest quarter) mm | 8 | 4 |

varied with the selection of outgroup species, the relationships between the most external members of the *S. macroura* clade (*S. bindi*, *S. archeri*, *S. butleri*, *S. virginiae* and *S. douglasi*) remained robust. The affinities of *bindi* lie with this 'broad-faced' sub-clade of dunnarts of which it is the most plesiomorphic species and of which *S. virginiae* and *S. douglasi* are the most derived.

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PARANDRA ARAUCARIAE GRESSITT (COLEOPTERA: CERAMBYCIDAE:
PARANDRINAE): A NEW RECORD FOR NORFOLK ISLAND

G.A. WEBB

Webb, G.A. 1994 12 01; *Parandra araucariae* Gressitt (Coleoptera: Cerambycidae: Parandrinae): a new record for Norfolk Island. *Memoirs of the Queensland Museum* 37 (1):325-328. Brisbane. ISSN 0079-8839.

Parandra araucariae Gressitt is recorded from Norfolk Island for the first time. *Araucaria heterophylla* (Salisb.) Franco is confirmed as a larval host of *P. araucariae*. The current distribution of the genus *Parandra* in the Australasian region is related to the distribution of the plant genus *Araucaria* and to the palaeogeography of the region. □ *Coleoptera*, *Cerambycidae*, *Parandra*, *Norfolk Island*, *new record*.

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Parandra frenchi Blackburn is the only species of *Parandra* described from Australia and its territorial islands. Several species are present in New Guinea, and adjoining islands and in the island groups of Fiji and New Caledonia (Arigony, 1984; Bigger & Schofield, 1983). In the early 1970's the collections of both the Forestry Commission of New South Wales in Sydney (FCNI) and the Australian National Insect Collection in Canberra (ANIC) acquired female specimens of a small *Parandra* from Norfolk Island, 1200km east of Brisbane. These have now been identified as females of *Parandra araucariae* Gressitt, a species formerly only known from New Guinea and Normanby Is., off the south-east coast of New Guinea (Bigger & Schofield, 1983; Gressitt, 1959)

OBSERVATIONS

MATERIAL EXAMINED

Norfolk Island: Taylors Rd, 1 Feb 1973, K. Clarke, ex. Norfolk Island Pine sawn timber, 3F, FCNI; Dec 1984, M. Jowett, F, ANIC; Mar 1971, 'Donated by residents of the island', F, ANIC; Botanic Garden, May 1984, L. Hill, ANPWS, F, ANIC; R. Paton, 7 Feb 1980, in *Araucaria* log, F, ANIC; R. Paton, 7 Feb 1980, in fungus, F, ANIC; R. Paton, 5 Feb 1980, at light, F, ANIC.

New Guinea: NE, Wum, Upper Jimmi Valley, 840m, J.L. Gressitt, 16 Jul 1955, 1M - paratype, ANIC; Wau, H. Ohlms, Dec 1974, 1M, 1F, ANIC; Northern District, Bulolo, c. 638m, B.B. Lowery, 15 Jul 1970 to 4 Jan 1971, at light, 2F, ANIC.

REMARKS

Nine specimens (all females) from Norfolk Island and five from New Guinea (2 males and 3 females) were available for study. Female *P.*

araucariae appear to be highly variable in size ranging in body length from 8.7 to 17.5mm and maximum width (2.5 to 5.6mm) (Table 1 and Gressitt 1959). Specimens examined from Norfolk Island fall within the lower end of both of these ranges and are generally smaller using other criteria (Table 1). All specimens fit the original description in other respects.

DISCUSSION

HOST ASSOCIATION

Gressitt (1959) recorded the male and female type specimens 'on felled *Araucaria*' and other female material 'on *Araucaria*'. Gressitt gave no indication whether these specimens were reared from *Araucaria* timber or just found on timber. Gressitt and Hornabrook (1977) noted that 'The genus *Parandra* is associated with *Araucaria* trees in New Guinea'. Four specimens of *P. araucariae* collected from Norfolk Island were actually collected in *Araucaria heterophylla* (Salisb.) Franco timber or reared from stored timber, confirming the genus *Araucaria* as hosts of *P. araucariae*. One specimen was recorded 'in [unknown] fungus' but it is not clear whether this specimen was feeding on or in the fungus or whether it was in the decayed timber associated with a saprophytic fungus on *A. heterophylla*.

The locations provided by Gressitt (1959) and given for specimens in the ANIC from New Guinea fit within the distribution of both *A. cunninghamii* D. Don and *A. hunsteinii* K. Schum., the two species of *Araucaria* present in New Guinea (Enright, 1982). It is therefore not possible to determine which species of *Araucaria* was the host.

TABLE 1. Morphological characteristics of *P. araucariae* from Norfolk Island and New Guinea.

| CHARACTER | Mean and Range (mm) | | |
|--------------------------------------|-------------------------|---------------------|---------------------|
| | Norfolk Island (n = 9F) | New Guinea (n = 3F) | New Guinea (n = 2M) |
| Body length | 12.2 (8.7-17.1) | 14.1 (13.0-15.2) | 14.6 (13.6-15.6) |
| Elytron length | 7.9 (5.4-10.3) | 8.7 (8.2-9.6) | 8.4 (8.0-8.8) |
| Elytron width at base | 3.4 (2.5-4.6) | 4.0 (3.6-4.4) | 4.1 (3.8-4.4) |
| Head width (to edge of eye) | 2.9 (2.2-3.6) | 3.1 (2.8-3.5) | 3.8 (3.6-4.0) |
| Pronotum length | 2.7 (2.0-3.6) | 2.9 (2.7-3.3) | 3.4 (3.1-3.6) |
| Pronotum width | 3.4 (2.5-4.3) | 3.9 (3.7-4.2) | 4.3 (4.0-4.6) |
| Antenna length | 3.0 (2.5-3.8) | 3.3 (3.2-3.5) | 3.7 (3.6-3.8) |
| Antenna/body ratio | 0.24 (0.24-0.29) | 0.24 (0.23-0.25) | 0.25 (0.24-0.26) |
| Head width/body length ratio | 0.23 (0.21-0.30) | 0.22 (0.21-0.23) | 0.26 (0.26-0.26) |
| Pronotum width/pronotum length ratio | 1.29 (1.25-1.36) | 1.33 (1.27-1.37) | 1.29 (1.28-1.29) |
| Elytra width/elytra length ratio | 0.43 (0.35-0.47) | 0.46 (0.44-0.48) | 0.49 (0.48-0.50) |

Species of *Parandra* have been recorded from a range of plant hosts (Duffy, 1960, 1963; Gressitt 1959). To my knowledge, four species have been recorded from *Araucaria* hosts (Table 2).

PALAEOGEOGRAPHIC DISTRIBUTION OF *ARAUCARIA* AND *PARANDRA*.

The palaeogeography of Gondwanaland is of considerable significance in interpreting the present day distribution of *Araucaria* and *Parandra*. Both genera are distributed largely on the southern blocks which once formed Gondwanaland (Africa, South America, and the Australasian region). *Araucaria* has a limited distribution in the southern hemisphere occurring in Australia (including Norfolk Is.), Papua New Guinea, New Caledonia, New Hebrides and in South America (Ntima, 1968). To a limited extent, *Parandra* has spread beyond these limits into central and North America from South America, and into South-east Asia from the Australian region via New Guinea. *Parandra* also occurs on the African continent, where *Araucaria* is now absent.

The first *Araucaria* fossils appeared in the lower Jurassic (180-160mya) of southern India, New Guinea, eastern Australia, New Zealand and Antarctica (Ntima, 1968). The genus survived on

the Indian and New Zealand blocks until the end of the Mesozoic (135-125mya) (Crook, 1981; Powell et al., 1981), about the time when India separated from Gondwanaland. The New Zealand block (containing New Zealand, New Caledonia, Fiji, Lord Howe Island and Norfolk Island) separated from continental Australia in the late Cretaceous (c. 80-60mya) but maintained a tenuous land bridge through the northern end of the Lord Howe Rise (off Queensland). Species of *Araucaria* and *Parandra* persist on all of these islands/island groups except New Zealand and Lord Howe Island.

Final separation of Australia (and its leading edge which now forms part of New Guinea) from Antarctica occurred in the Oligocene (c. 35mya). South America remained connected to Antarctica till the early Tertiary (c. 60mya) (Barlow, 1981) but Raven (1979) considered that final separation may have occurred as late as the Oligocene (c. 38-27mya), around the time Australia finally separated from Antarctica. Nevertheless, both continents remained connected via Antarctica until well after the first fossil evidence of *Araucaria*.

Thus, the presence of *Araucaria* in the Australasian region and in distant South America can be explained by the relatively late separation of both blocks from Antarctica. Similarly, within

TABLE 2. Araucarian hosts of *Parandra* spp.

| <i>Parandra</i> spp. | Distribution | Host (and reference) |
|-------------------------------|----------------------------|---|
| <i>P. araucariae</i> Gressitt | New Guinea, Norfolk Island | <i>A. cunninghami</i> D. Don or <i>A. hunsteinii</i> Schum. (Gressitt, 1959). <i>A. heterophylla</i> (Salib.) Franco (this study) |
| <i>P. frenchi</i> Blackburn | Eastern Australia | <i>A. cunninghamii</i> D. Don (Ildidge, 1924) |
| <i>P. araucana</i> Bosq. | South America | <i>A. araucana</i> (Mol.) K. Koch (Duffy, 1960) |
| <i>P. glabra</i> (Degeer) | South America | <i>A. angustifolius</i> (Bertol.) Kuntze (as <i>brasiliensis</i>) (Duffy, 1960) |

the Australasian region connections between Antarctica and the present day locations of *Araucaria* (Australia, New Guinea, Norfolk Island, New Caledonia, Vanuatu) remained until well after the period of first emergence of *Araucaria*.

DISTRIBUTION AND RELATIONSHIPS

Parandra is currently known from the Australasian region, South-east Asia, South and North America, and Africa. Eight species of *Parandra* (all from the subgenus *Parandra*) are known from the Australasian region and south-east Asia (Arigony, 1984). Based on detailed study of the morphology of these species, Arigony designated three groups within the subgenus *Parandra*. Group 1 contained *P. frenchi* Blackburn (Australia) and *P. araucariae* Gressitt (New Guinea, Normanby Is. and now Norfolk Is.) while Group 3 contained: *P. passandroides* Thomson (New Caledonia), *P. austrocaledonica* Montrouzier (New Caledonia), *P. heterostyla* Lamcere (Celebes), *P. solomonensis* Arigony (Solomon Islands) and *P. janus* Bates (New Guinea northward). The position of *P. striatifrons* Fairemaire (Fiji) was not discussed but it probably fits within group 3. Group 2 contains South American and African species and will not be considered further.

P. araucariae is known from New Guinea and from Normanby Island immediately southeast of the mainland of New Guinea (Arigony, 1984; Bigger & Schofield, 1983; Gressitt, 1959). Norfolk Island is c. 2700km SE of the previously known distribution for *P. araucariae* and is closer to Australia (c. 1200km), Fiji (c. 1600km) and New Caledonia (ca. 700km) than to New Guinea. Two species of *Parandra*, *P. austrocaledonica* and *P. passandroides*, are known from New Caledonia and one species, *P. striatifrons*, from Fiji.

Curiously, no *Parandra* were identified from the entomological collections from Norfolk Island detailed by Olliff (1888) and Hawkins (1942). This lack of previous evidence of its presence on Norfolk Island, the geographical distance from its previously known distribution and the absence of *P. araucariae* and other group 1 *Parandra* (*Parandra*) (sensu Arigony, 1984) from other islands of the New Zealand block invites some suspicion about its status on Norfolk Island. *P. araucariae* may have been accidentally introduced to Norfolk Island in timber (although there is no clear evidence of this).

Alternatively, it may represent a relict population of *P. araucariae* which may have been more widespread in the past (although there is no fossil evidence to support this either) or it may represent a new species closely allied to *P. araucariae*. Further study on a larger sample (including males) is required.

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TAXONOMY OF *POGONA* (REPTILIA: LACERTILIA: AGAMIDAE)

G.J. WITTEN

Witten, G.J. 1994 12 01: Taxonomy of *Pogona* (Reptilia: Lacertilia: Agamidae). *Memoirs of the Queensland Museum* 37(1): 329-343. Brisbane. ISSN 0079-8835.

Pogona is distinctive and contains six species of moderate to large agamid lizards. *P. barbata*, *P. microlepidota*, *P. nullarbor* and *P. vitticeps* are retained as proposed by Badham (1976). *P. minor* is a widely distributed polymorphic species with subspecies retained in the form proposed by Storr (1982). *P. brevis*, a species similar in size to *P. minor* and *P. nullarbor* but with shorter appendages, is described from the 'black soil' plains of central Queensland. *P. brevis* retains more primitive features than any other species. *P. microlepidota* is closely related to, but distinct from, *P. minor*. *P. nullarbor* and *P. barbata* are the most derived species of the genus, the former probably being closer to their common ancestor in form. Morphological variation within *P. minor* indicates a close relationship with the *Amphibolurus* radiation and *Chlamydosaurus*. An animal similar to *P. minor* is a probable progenitor of both, although the two derived taxa seem to have evolved separately. □
Reptilia, Agamidae, Pogona, taxonomy, new species, phylogeny.

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Pogona was described by Storr (1982) to accommodate the bearded dragons, a discrete group of agamids which occur almost Australia-wide, with a single species of the genus in most areas. Once thought of as a widespread polymorphic species, Badham (1976) was able to demonstrate specific differences within the complex, resurrecting *P. vitticeps* from the synonymy of *P. barbata*, and describing several new species. Storr (1982) redefined some of the taxa used by Badham, reducing *P. mitchelli* and *P. minima* to subspecies of *P. minor*. Witten (1982b) suggested *Pogona* evolved from a species similar to *Ctenophorus nuchalis*, but no other phylogenetic relationship has been suggested. An attempt is made here to further stabilise our understanding of the taxa within *Pogona*, and to explore the probable relationships between it and other agamid genera.

MATERIALS AND METHODS

Meristic characters were recorded with the aid of a binocular dissecting microscope. Labial scales were counted forward from the angle of the mouth, excluding some large scales which continue the 'supralabial' series posteriorly. Subdigital lamellae under the fourth toe were counted from the junction of the third and fourth toe. Where possible, counts are from the right side of the body. For features which vary within a taxon the proportion of specimens scored with the feature is presented as a part of unity (e.g. 0.60 to indicate 60% of specimens with a particular fea-

ture). All features were not scored from all specimens. Specimens used in this study are housed in the Australian Museum, Sydney (AM); Museum of Victoria (NMV); South Australian Museum (SAM); and the Western Australian Museum (WAM).

SYSTEMATICS

Pogona Storr, 1982

DIAGNOSIS

Pogona can be distinguished from all other Australian agamids by the presence of spinose scales along the lateral margin of the trunk, and the absence of both vertebral and paravertebral rows of enlarged scales on the trunk.

DESCRIPTION

Moderate to large agamids (120-250mm maximum snout-vent length). Short limbs and tail relative to most other agamids. Head deep with blunt snout. Lacrimal bone absent, but lateral process of palatine may intrude into antero-inferior angle of orbit. Preanal and femoral glands widely spaced and arching forward on antero-ventral surface of thigh. Pores usually appear to penetrate skin between scales, but are in fact normally contained within the posterior part of a slightly enlarged scale, commonly appearing in a notch on the posterior margin. Premaxilla narrow, with 3 teeth in adults unless there are replacement teeth developing. Up to 3 pleurodont teeth at the front of both the maxilla and dentary.

Paramarginal scales of lower eyelids with spines which increase in relative size ontogenetically. Gular pouch enlarged. Transverse series of spinose scales at least in lateral gular region, continuing up behind the angle of mouth and tympanum. An occipital crest formed by a series of spines running medially, and at least slightly anteriorly, from about the posterior border of the parietal bone. Temporal series of enlarged scales above tympanum. Scapular tubercle formed by a group of spinose scales at the lateral extension of the gular fold, in front of the insertion of the forelimb. A skin fold from behind the tympanum extends medially to a group of spinose scales on an area of raised skin, either as a fold or tubercle. Nuchal crest is never well developed, but a row of enlarged scales in the nuchal midline is present in some individuals of all species. There may also be a longitudinal paravertebral series of enlarged scales on the neck. Dorsal trunk scales strongly heterogeneous, the central scales much enlarged to form a raised 'farrier's rasp'. Dorsolateral scales much smaller, with scattered spinose scales, and separated from the ventrals by one or more series of spinose scales along the lateral margin of the trunk. Vertebral scale ridge absent. Labials usually smooth, about as long as deep. Loreal scale row obscure in adults. Tympanum large, without scales, at the end of a short meatus restricted postero-superiorly by a skin fold. Canthus rostralis acute to sharply rounded, nares below. Permanent black ventral markings absent; ventral surface marked with dark ocellations. Dorsal colouration consisting of light and dark grey pattern. Colour pattern fades with increase in size. Strongly metachromatic, varying from almost black to light ashen grey in the same individual. Karyotype $2n = 32$ (12M, 20m).

Pogona barbata (Cuvier, 1829)

Agama barbata Cuvier, 1829: 35.

Pogona barbata Storr, 1982: 201.

MATERIAL EXAMINED

AMR17904, AMR21578, AMR25789, no data; New South Wales: AMR59988, AMR59990, East of West Wyalong; AMR59989, 51 km East of Grenfell; AMR59992, 33km SW Hillston; AMR107399-400, AMR107412-3, Upper Horton area; AMR107401, 26 km N Euabalong West; AMR107407-8, AMR107411, 41-50km W Grenfell; NMVD151, Finley; NMVD896, Deniliquin; NMVD14034, 71km W of Moree; NMVD14036, 32km from Moree; Queensland: AMR107397, AMR107402, Emerald; AMR107403, 40m NE Clemmont; AMR107404, 25m E Charters

TABLE 1. Meristic characters of *Pogona barbata*.

| Scale Count (n) | Mean (SD) | Range |
|-----------------------|--------------|---------|
| Prenasals (27) | 4.63 (0.63) | 4-6 |
| Subnasals (27) | 4.07 (0.68) | 3-5 |
| Internasals (27) | 10.30 (1.03) | 9-13 |
| Rostral-parietal (26) | 14.50 (1.59) | 12-18 |
| Suborbitals (27) | 4.33 (0.48) | 4-5 |
| Supralabials (27) | 17.07 (1.24) | 14-19 |
| Infralabials (27) | 16.26 (1.20) | 14-18 |
| Mid-body scales (21) | 141.1 (15.6) | 101-175 |
| Lamellae (27) | 22.74 (1.93) | 18-26 |
| Pores (26) | 14.62 (2.06) | 11-19 |

Towers; AMR107405, Muttaborra; NMVD137, Fletcher; NMVD8038, Mt Emlyn via Milmerryn; QMJ49966, 5 km W Alpha; South Australia: AMR20987, Elliston, Victoria: NMVD723, "Goulbourne"; NMVD744, Great Western; NMVD966, Dunolly; NMVD1345; NMVD7934, Big Hill, Bendigo; NMVD14679, Puralka; NMVD14699, Kentbrook State Forest; NMVD48900, 30km South of Kaniva; NMVD57127, 10km ENE of Boort.

DIAGNOSIS

Distinguished by the presence of a complete multiple gular scale row of spinose scales, an area of spinose scales on the lateral trunk rather than a single interrupted series, and the absence of transverse light lines on the trunk.

DESCRIPTION

Occipital crests do not meet in the midline, but approach each other obliquely at an angle of about 120° to 130° . Occipital and temporal spine series continue off the posterior dorsum of the head, rather like the cushions of a billiard table, forming two parallel series descending behind the tympanum. Nuchal scale ridge present in about 50% of specimens. Gular scale row complete, formed by several rows of scales about 3 times as long as their base width in adults, the scales a little less attenuated in juveniles. Laterally the gular scale row becomes single and continues up behind the angle of the mouth to meet the temporal series and enclose a triangle of relatively smooth scales behind the tympanum. Spines of these series behind the tympanum are about 3 times as long as their base width. Lower tympanum is often hidden by loose skin. The postauricular skin fold carries spines from the posterior continuation of the occipital series, so the occipital crest forms a loop ending in the paravertebral group of spinose scales. A spine or two between the

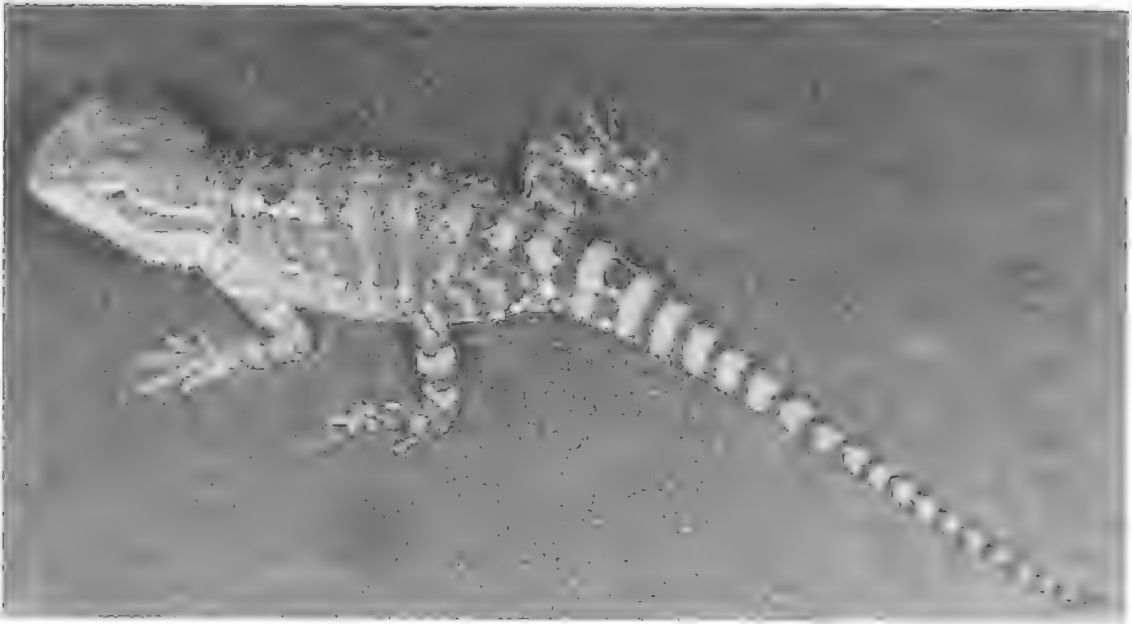


FIG. 1. Juvenile *Pogona brevis*. Specimen photographed in Melbourne Zoo.

posterior continuations of the temporal and occipital series may complete, with the gular series, a collar of spines interrupted only in the mid-dorsal region. Another series of spines in the gular region runs posteriorly along the inferior margin of the jaw behind the transverse gular scale row, but in front of the 'normal' gular fold. Scapular tubercle very prominent in large adults. Lateral scale row of trunk composed of scattered spines about 3 or 4 deep. Ventral scales keeled, more prominently in juveniles. Second ceratobranchials absent. Up to 250mm snout-vent length, Table 1 presents meristic data of the species.

***Pogona brevis* sp.nov.**

MATERIAL EXAMINED

HOLOTYPE: QMJ32292, adult, Croydon, Queensland. Collected D. Milton in June 1977. Snout-vent length 132mm, tail 141, snout-parietal distance 22.55, Snout-tympanum about 30.8; 15 supralabials, 14 infralabials, 5 scales between nasal and rostral, 5 scales between nasal and supralabials, 11 internasal scales and 18 from rostral to interparietal, 16 lamellae under right fourth toe, 17 under left. Seven preanal and femoral pores (3 left, 4 right).

PARATYPES: QMJ38735, Hughenden showgrounds; QMJ38760-1, Hughenden-Muttaburra road, QM J46949, Longreach; NMVD11164, South of Aramac; WAMR9856, Longreach.

OTHER MATERIAL: AM field series 11238, 11240, Aramac area; NMVD11165, Richmond; QMJ38762, Hughenden area. A series of animals held in Melbourne Zoo were also examined. The original locality of these animals is not known. Specimens 11238 and 11240 were lent to Richard Wells to assist him in describing the species. Their whereabouts are now not known.

DIAGNOSIS

Distinguishable from other *Pogona* by relatively short tail and limbs, and the low number of lamellae under the fourth toe (less than 18). The number of preanal and femoral glands is also reduced relative to other *Pogona* (12 or fewer).

TABLE 2. Meristic characters of *Pogona brevis*.

| Scale Count (n) | Mean (SD) | Range |
|-----------------------|--------------|--------|
| Prenasals (18) | 4.39 (0.61) | 3-5 |
| Subnasals (18) | 3.83 (0.51) | 3-5 |
| Internasals (17) | 10.88 (0.60) | 9-12 |
| Rostral-parietal (17) | 16.53 (1.97) | 14-21 |
| Suborbitals (17) | 4.12 (0.33) | 4-5 |
| Supralabials (17) | 14.59 (1.18) | 13-16 |
| Infralabials (17) | 13.71 (1.05) | 12-16 |
| Mid-body scales (16) | 106.0 (6.08) | 97-119 |
| Lamellae (19) | 16.47 (1.12) | 14-18 |
| Pores (17) | 8.18 (1.59) | 6-12 |

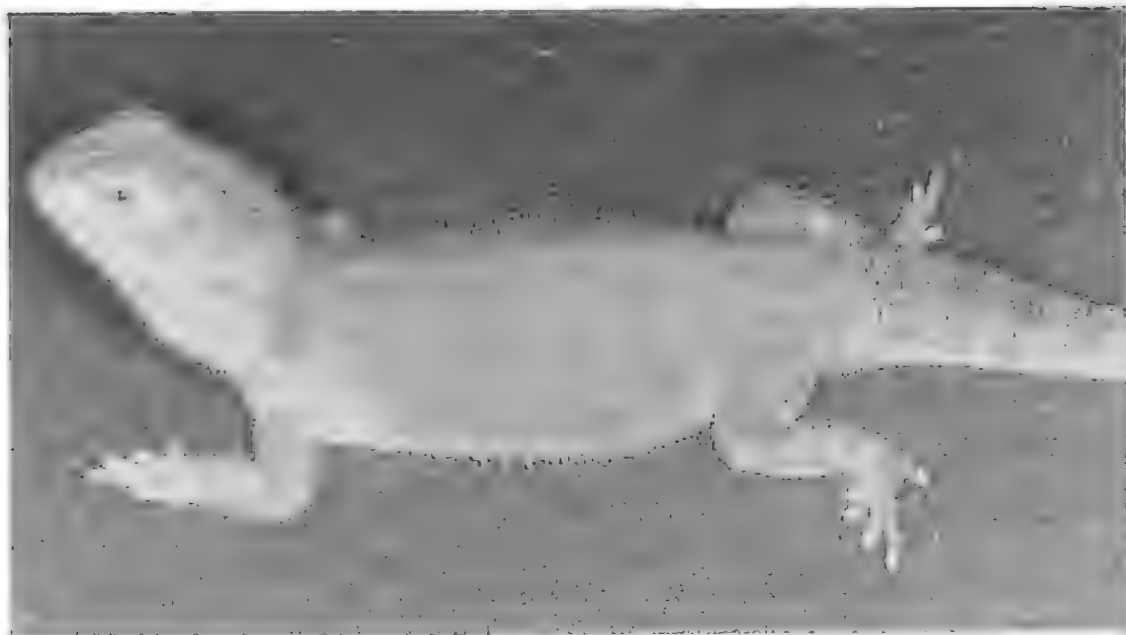


FIG. 2. Adult *Pogona brevis*. Specimen photographed in Melbourne Zoo.

DESCRIPTION

Medium-sized, males and females of similar size, adult males averaging 128.0mm SVL (range 91-148) females 130.8 (122-138). The occipital crest is not well developed but transverse, and would meet its fellow at about 150° if the two crests met in the midline. The temporal series approaches the lateral end of the occipital crest but does not continue behind the tympanum. A separate series of spines begins behind the tympanum and runs back to meet the lateral continuation of the gular series to enclose a triangle behind the lower half of the exposed part of the tympanum. The apex of this triangle continues medially as spines on the postauricular fold to a small group of tubercles on the side of the neck. The gular series is very poorly developed and absent in some individuals. The postauricular spines are less than 3 times their base width. Nuchal crest present in only two of 19 specimens examined. Paravertebral nuchal scale row usually present. The scapular tubercle is not well developed. The lateral spines of the trunk are 2 to 3 times their base width. The series is not well developed; there are usually 3 or 4 smaller scales between successive spines. Farrier's rasp condition not well developed, dorsal tubercles more regularly arranged than in other *Pogona*. A small orange area below the tympanum, hidden at times by skin fold. Colour pattern typical of *Pogona*

(Fig. 1), less distinct in larger specimens (Fig. 2). Second ceratobranchials present. Meristic data of the species are presented in Table 2.

ETYMOLOGY

From the Latin *brevis* = short, referring to the relatively short limbs, tail, and snout.

REMARKS

Pogona henrylawsoni Wells & Wellington (1985) cannot be identified from available information. Wells & Wellington's 'diagnosis' apparently includes a description of the holotype, a diagnosis for the species as well as a general description. It is not clear where each of these begins or ends. The description given is not adequate to distinguish *P. henrylawsoni* from other species of *Pogona*. The first diagnostic character given is 'Snout to vent length 130.0mm; vent to tail length 117.0mm'. Taken literally this should exclude all specimens smaller or larger, but even the proportions given would exclude all *P. brevis*; no specimen I examined had an intact tail shorter than the snout vent length. Wells & Wellington (1985) give a full description of the colour pattern, which could apply to any member of the genus. Another 'diagnostic feature' is that *P. henrylawsoni* has smooth ventrals compared to keeled ventrals in *P. vitticeps*. Ventrals in *P. vitticeps* are usually keeled (0.69), but are quite

smooth in some specimens. About half the specimens of *P. brevis* I examined had keeled ventrals. Further, the specimen nominated as the holotype, Australian Museum Field No. 16814, could not be located in a series of specimens donated to the Australian Museum by Wells (Sadleir, pers. comm.). Another specimen mentioned as a '*P. henrylawsoni*', QMJ1051, has apparently been lost (Couper, pers. comm.). There are therefore no known specimens assigned to *P. henrylawsoni* which might act as a guide to the intentions of the authors. As the most common *Pogona* from the type locality of *P. henrylawsoni* is *P. vitticeps*, I treat it as a junior synonym of *P. vitticeps*. A neotype for *P. henrylawsoni* is nominated under the description of that species.

This species is referred to as dwarf bearded dragon. The name is not entirely appropriate, as it attains larger size than *P. minor minor* and *P. nularbor*. However, it is sympatric with both 'giant' species of *Pogona*, and is certainly small relative to those species. A more appropriate name would be 'downs bearded dragon'. People from central Queensland refer to the black soil habitat of *P. brevis* as downs country.

Little is known of the species' ecology. The two specimens I collected were on a dirt road in black soil country. Despite spending several months in the Aramac area I never saw *Pogona* of this size perching on fence posts. It is possible that *P. brevis* defends territory without the normal perching behaviour of other *Pogona*. Almost half the other specimens in museum collections were road kills, also suggesting the species is not obvious to passing herpetologists.

Pogona microlepidota (Glauert, 1952)

Amphibolurus barbanus microlepidotus Glauert, 1952: 168.
Amphibolurus microlepidotus Badham, 1976: 439, fig. 4f.
Pogona microlepidota Storr, 1982: 211.

MATERIAL EXAMINED

WAMR43028, WAMR56232, Crystal Head; WAMR44258, Mitchell Plateau; WAMR46847, WAMR46962, Prince Regent River National Park; WAMR57108, Bigge Island.

DIAGNOSIS

Distinguished by the presence of a multiple lateral scale row, and a weakly developed gular scale row, with no differentially spinose scales in the central throat region.

TABLE 3. Meristic characters of *Pogona microlepidota*.

| Scale Count (n) | Mean (SD) | Range |
|---------------------|--------------|---------|
| Prenasals (6) | 5.50 (0.84) | 4-6 |
| Subnasals (6) | 4.00 (0.89) | 3-5 |
| Internasals (6) | 12.00 (0.89) | 11-13 |
| Rostral-panetal (6) | 19.17 (1.17) | 18-21 |
| Suborbitals (6) | 4.67 (0.52) | 4-5 |
| Supralabials (6) | 16.50 (1.38) | 15-18 |
| Infralabials (6) | 14.17 (1.47) | 12-16 |
| Mid body scales (6) | 124.3 (8.57) | 116-139 |
| Lamellae (6) | 22.67 (0.52) | 22-23 |
| Pores (5) | 11.50 (1.64) | 10-14 |

DESCRIPTION

Gular scale row incomplete, reduced to a few spinous scales below the tympanum. Occipital crest transverse, often on raised skin fold, but not formed by greatly enlarged scales, not extending laterally to meet temporal series nor its fellow in midline. Postauricular fold passes medially to raised area of skin embossed with tubercles; usually a second raised group of tubercles between this and the midline. Ventral and gular scales strongly keeled and mucronate. Lateral scale row of several rows of enlarged spinous scales. Second ceratobranchials present. Up to 180mm snout-vent length (Storr, 1982). Meristic data are presented (Table 3).

Pogona minor minor (Sternfeld, 1919)

Amphibolurus barbatus minor Sternfeld, 1919: 78.
Amphibolurus minor Badham, 1976: 436, fig. 4d.
Pogona minor Storr, 1982: 203.
Pogona lorae Wells & Wellington, 1985: 19

MATERIAL EXAMINED

'Typical' *Pogona minor minor*: South Australia: AM R5660-1, Port Lincoln; AMR7658, 407 miles East West line, 30°30'S, 132°09'E; NMVD2657, NMVD2979, NMVD3010, Overland Railway, W of Kychering Soak; NMVD3037, NMVD3052, Overland Railway; NMVD65339, NMVD65379, Wirrula area; NMVD65361, Peterby Tank; SAMR587, Everard Ranges; SAMR5312, Mount Davies; SAMR6556, Yalata Mission; SAMR14482, Maralinga; SAMR14635, Ammaroodinna Hill; SAMR14955A-C, Mt Finke; SAMR14986A-C, Immarna; SAMR15004A-D, Koonibba Mission; SAMR15304, Pinkawillinie Conservation Park; SAMR15506, Emu; SAMR15568, Wyola Lakes; SAMR15569, 74 miles West Vokes Hill; SAMR18132, Muckera Rock Hole; SAMR18133, Serpentine Lakes; SAMR18168-9, Wyola Lakes; SAMR18376, Vokes Hill Junction; SAMR21374, Bates; SAMR22914-5, Yallata Mission area; SAMR24479, Goog's track;

SAMR25427, 45 Canegrass Swamp; SAMR25428, Mt Ive Homestead; SAMR25673, 51km NW Yalata Rockhole; SAMR26389, 99km NW Cook; SAMR26809, Mabel Creek homestead; SAMR28437, 45km NNE Minnipa; SAMR28525, 100km NE Minnipa; SAMR30083, Yalata; SAMR31872, SAMR31875, Mt Finke; SAMR31916, SAMR31923, Pinjarra Dam; SAMR31939-40, Wallala Hill; SAMR31961, Inila Rock Waters, Yumbarra Conservation Park; SAMR31989, Yumbarra Rock Hole; SAMR32011, SAMR32019, Mitcherie Rock hole; SAMR32036-8, SAMR32073, SAMR32076, SAMR32095, Immarina Siding; SAMR32142, SAMR32146, SAMR32165, SAMR32174, Maralinga; SAMR32189, 47km N Muckera Rockhole; SAMR32205, SAMR32214, SAMR32218, SAMR32279, 50km SW Halinor Lake; SAMR32288, 29km N Muckera Rockhole; SAMR32312, Mt Christie Siding; SAMR32613, Two Tik Bore; SAMR32622, Tallaringa Well; SAMR33983, Mt Pinke; SAMR36226, Curtin Springs homestead; SAMR37656, 39km S Kokatha homestead, Northern Territory; AMR15182, Haast's Bluff, Macdonnell Range; NMVD493, Illamurra; SAMR322, Macdonnell Ranges; SAMR4820, Mt Liebig; SAMR9520, Yuendumu; SAMR29903, Curtin Springs homestead; WAMR34182, Armstrong Creek; WAMR34197-8, Lasseter's Cave; WAMR45206, Docker River; WAMR46634-5, Ayer's Rock, Western Australia; SAMR1402A-D, between Ashburton and Gascoyne Rivers; WAMR19568, Ullawarra; WAMR31004, Mount Tom Price.

Pogona minor 'minima' morphs; Western Australia; AMR133759, Gibson; AMR133915, AMR133988, Salmon Gums; AMR136236, Nedlands; AMR136239, Lesmurdie; NMVD772-4, King George Sound; NMVD2435, Katarnting; NMVD8002, Bunbury; SAMR22836, Yanchep; WAMR23812, Field's Find; WAMR37737, 29km ENE Paynes Find; WAMR87461, Lake Mason homestead.

Pogona minor 'minima/minor' intermediates not used in preliminary analyses: AMR134278, AMR134565, Gnaratoo Bay; AMR134313, AMR134584, Point Quobba; AMR136238, Vlaming Head; AMR136240, 57m NE Fraser Range turn-off, Nullarbor Plain; SAMR25494, 87km NW Cook; SAMR25577, 82km NW Cook; SAMR25678, 50 km W Yalata rockhole; NMVD783-5, Minilya; NMVD976, Stanton Springs; NMVD1778, Middalya; NMVR849, NMVR852, NMVR1005, NMVR1007, NMVR1011, (?)Perth; WAMR16867-71, Ningaloo; WAMR19567, Wittenoom; WAMR24829, Landor; WAMR29965-7, Overlander; WAMR69679, Mount Bruce; WAMR70808, Dirk Hartog Island; WAMR78246-7, Boolgoopo.

Pogona minor 'minima' morphs not included in analyses: NMVD630, NMVD664-8, NMVD782, NMVD3405, Western Australia; NMVR848, NMVR1002, NMVR1004, NMVR1006, NMVR1008, (?)Perth.

TABLE 4. Meristic characters of *Pogona minor minor*.

| Scale Count (n) | Mean (SD) | Range |
|-----------------------|--------------|--------|
| Prenasals (78) | 4.79 (0.81) | 3-7 |
| Subnasals (78) | 3.82 (0.58) | 2-5 |
| Internasals (77) | 10.13 (1.22) | 7-13 |
| Rostral-parietal (74) | 13.92 (1.29) | 12-18 |
| Suborbitals (77) | 3.84 (0.48) | 3-5 |
| Supralabials (81) | 15.79 (1.30) | 13-19 |
| Infralabials (81) | 14.65 (1.28) | 11-17 |
| Mid-body scales (35) | 109.7 (7.60) | 99-127 |
| Lamellae (78) | 23.81 (2.26) | 16-28 |
| Pores (101) | 13.42 (1.75) | 10-18 |

DIAGNOSIS

P. minor is distinguishable from other *Pogona* by the presence of gular scales similar to ventrals, without a transverse series of more spinose scales at the centre of the throat; a single interrupted series of spinose scales along the lateral margin of the trunk, and a relatively long tail (at least 160% of snout-vent length). *P. m. minor* has a weaker occipital crest and narrower head than at least adult *P. m. mitchelli*, and shorter appendages than *P. m. minima*.

DESCRIPTION

Occipital crest transverse, but not strongly developed. Temporal series of spines does not continue much behind level of tympanum. The postauricular skin fold ends medially in a variable paravertebral structure. From the north and east of the species' range there is a raised area of skin supporting a clump of tubercles, often in the form of a large single scale surrounded by smaller spines. Specimens from the west of the species' range have a skin fold running forward from the medial end of the postauricular fold carrying a more or less longitudinal row of tubercles. Nuchal scale ridge often present (0.60). Gular scale row incomplete. Ventrals weakly keeled (0.60) or smooth, gulars weakly keeled (0.30) or with a rounded surface. Preanal and femoral glands much more active in males than females. Second ceratobranchials present. Up to 145mm snout-vent length (Badham, 1976). Table 4 presents meristic data of the nominate subspecies, including specimens from the south-west of Australia.

Pogona minor minima (Loveridge, 1933)

Amphibolurus barbatus minimus Loveridge, 1933: 69.
Amphibolurus minimus Badham, 1976: 437.

Pogona minor minima Storr, 1982: 208.

TABLE 5. Meristic characters of *Pogona minor minima*.

| Scale Count (n) | Mean (SD) | Range |
|-----------------------|--------------|--------|
| Prenasals (16) | 4.44 (0.51) | 4-5 |
| Subnasals (16) | 3.06 (0.25) | 3-4 |
| Internasals (16) | 9.50 (1.32) | 7-13 |
| Rostral-parietal (16) | 12.75 (1.18) | 11-15 |
| Suborbitals (16) | 3.13 (0.34) | 3-4 |
| Supralabials (16) | 14.00 (1.03) | 12-16 |
| Infralabials (16) | 13.63 (0.81) | 12-15 |
| Mid-body scales (11) | 100.3 (9.46) | 82-120 |
| Lamellae (16) | 24.69 (1.62) | 22-28 |
| Pores (12) | 14.58 (1.83) | 12-17 |

MATERIAL EXAMINED

WAMR19501-16, West Wallabi Island.

DIAGNOSIS

Distinguished from the nominate subspecies by the possession of longer appendages, the forelimb length falling from about 50% to 44% of snout vent length during growth (44% to 37% for *P. m. minor*), and from *P. m. mitchelli* by a much narrower head (less than 23% of snout vent length in large adults) and weak development of the occipital crest.

DESCRIPTION

Postauricular fold medially joins a longitudinal skin fold with a series of enlarged spines. Labial scales frequently carry a longitudinal ridge, particularly the posterior supralabials. All scales keeled, gulars weakly. Up to 115mm snout-vent length (Storr, 1982). Meristic data are presented in Table 5.

REMARKS

Badham (1976) treated both *P. m. minima* and *P. m. mitchelli* as full species. Storr (1982) reduced both to subspecies of *P. minor*. Storr also altered the boundary between *P. minima* (of Badham) and *P. minor*, restricting *P. m. minima* to the type locality of the holotype, the Houtman Abrolhos Islands.

Badham (1976) used the presence of a 'distinct nuchal row of 5 or 6 spines parallel to and on either side of the vertebral column' as the main feature characterising *P. minima*. Using this character, I sorted mainland specimens into 'minima' morphs and *P. m. minor*. Animals intermediate in morphology or distribution were excluded. Analyses of morphometric and meristic data were carried out. The morphometric data are discussed

elsewhere (Witten, 1994), and the meristic data are presented in Table 6.

Storr (1982) used the higher number of lamellae under the fourth toe as one feature helping to distinguish *P. m. minima* from *P. m. minor* on the adjacent mainland. My data show a lower number of lamellae in the mainland 'minima' morph group, but the number of lamellae in *P. m. minor* from other areas is close to identical to that of *P. m. minima*. Storr's data had a slightly higher mean for Houtman Abrolhos animals (25.3) and a lower one for mainland *P. m. minor* (22.8) than I recorded, but even Storr's data could only be used diagnostically at the extremes of his recorded ranges. Other data recorded do not show any significant difference between groups. There is a tendency for Houtman Abrolhos specimens to have fewer scales between the labials and both the orbit and nasal scale. The number of labial scales is lower in the island population, but there are more preanal and femoral glands (Table 6). Both these trends are consistent with Storr's data. The meristic data do not show a consistent trend indicating whether the mainland 'minima' animals should be grouped with *P. m. minor* or *P. m. minima*. However, analyses of morphometric data support Storr's position (Witten, 1994). The data presented with the description of *P. m. minor* include all mainland specimens examined, apart from those assigned to *P. m. mitchelli*.

TABLE 6. Meristic characters of *Pogona minor*. Numbers in each column are mean (SD) and range.

| Count | <i>P. m. minor</i> | <i>P. m. minima</i> mainland | <i>P. m. minima</i> |
|------------------|----------------------|---------------------------------|----------------------|
| Prenasals | 4.86(0.78) 3-7 | 4.43(0.85) 3-6 | 4.44(0.51) 4-5 |
| Subnasals | 3.82(0.57) 3-5 | 3.71(0.73) 2-5 | 3.06(0.25) 3-4 |
| Internasals | 10.23(1.26) 8-13 | 9.64(1.22) 7-12 | 9.50(1.32) 7-13 |
| Rostral-parietal | 13.98(1.33) 12-18 | 13.64(1.43) 12-16 | 12.75(0.18) 11-15 |
| Suborbitals | 3.80(0.48) 3-5 | 3.93(0.47) 3-5 | 3.13(0.34) 3-4 |
| Supralabials | 15.90(1.32) 13-19 | 15.14(1.10) 13-17 | 14.00(1.03) 12-16 |
| Infralabials | 14.77(1.20) 12-17 | 14.14(1.29) 11-15 | 13.63(0.81) 12-15 |
| Mid-body scales | 110.6(7.3) 99-127 | 102.8(1.8) 101-105 | 100.3(9.5) 82-120 |
| Lamellae | 24.11(2.05) 19-28 | 22.69(3.15) 16-28 | 24.69(1.62) 22-28 |
| Pores | 13.54(1.72) 10-18 | 12.85(2.03) 9-16 | 14.58(1.83) 12-17 |

TABLE 7. Meristic characters of *Pogona minor mitchelli*.

| Scale Count (n) | Mean (SD) | Range |
|-----------------------|--------------|--------|
| Prenasals (30) | 4.67 (0.71) | 3-6 |
| Subnasals (30) | 4.30 (0.75) | 3-6 |
| Internasals (30) | 10.97 (1.33) | 9-13 |
| Rostral-parietal (30) | 15.10 (1.94) | 11-20 |
| Suborbitals (30) | 4.17 (0.65) | 3-6 |
| Supralabials (30) | 15.80 (1.30) | 14-19 |
| Infralabials (30) | 14.87 (1.11) | 13-17 |
| Mid-body scales (14) | 110.6 (9.20) | 90-122 |
| Lamellae (30) | 22.10 (1.7) | 19-27 |
| Pores (28) | 13.21 (1.87) | 10-18 |

***Pogona minor mitchelli* (Badham, 1976)**

Amphibolurus mitchelli Badham, 1976: 435, fig. 4c.
Pogona minor mitchelli Storr, 1982: 209.

MATERIAL EXAMINED

PARATYPES: Northern Territory: SAMR1399-1400, SAMR1404, Tennant Creek; SAMR3546, Yuendumu. Western Australia: SAMR3436, Pilgangoora Well; WAMR13066, Mount Edgar; WAMR15823, Derby; WAMR19377, Mundabullangana.

OTHER MATERIAL: Northern Territory: SAMR15622, Yuendumu. Western Australia: AMR38712, 11m W Springvale; AMR100912-5, AMR101470-1, AMR101550, Sandfire Flat roadhouse; NMVD999, Broome; NMVD1000-1, Marble Bar; WAMR45758-60, Mount Edgar; WAMR46068, 63km ENE de Grey River crossing; WAMR50696, Drysdale River National Park; WAMR68983, 24km E Deep Creek; WAMR79111-2, Broome; WAMR87344, Mandora homestead.

OTHER SPECIMENS (examined, but not used in analyses): SAMR4483, Tambrey; SAMR4484, Kangiangi, W.A.; WAMR20078-9, Tambrey, W.A. (These specimens are all paratypes of *Amphibolurus mitchelli*, but are actually *P. m. minor* - see Discussion); NMVD33, NMVD2949, Tennant Creek N.T.; NMVD494, Ilamurra, N.T.; NMVD1480, Derby, W.A.; NMVR847, NMVR850, NMVR1009-10, Perth(?), W.A.

DIAGNOSIS

Distinguished mainly by the possession of a prominent transverse occipital crest similar to *P. vitticeps*, and a relatively wider head and larger ear aperture than other *P. minor*.

DESCRIPTION

Similar in most respects to *P. m. minor*. Ventrals weakly keeled (0.67) or smooth, gulars weakly keeled (0.33) or with a rounded surface.

Up to 171mm snout-vent length. Meristic data of the subspecies are presented in Table 7.

***Pogona nullarbor* (Badham, 1976)**

Amphibolurus nullarbor Badham, 1976: 440, fig. 4g.
Pogona nullarbor Storr, 1982: 212.

MATERIAL EXAMINED

PARATYPES: WAMR16888, WAMR16896, Forrest; WAMR24655, Cocklebiddy; WAMR28127, Wilson Bluff; WAMR31964-5, 112 km NNE Rawlinna.

OTHER MATERIAL: South Australia: SAMR5034, Eyre Peninsula or Nullarbor Plain; SAMR14313A-B, 29km S Watson; SAMR14314, Watson; SAMR15570, 10m E Cook; SAMR18170, SAMR19807, SAMR20106, SAMR22290, SAMR23939-41, SAMR25298-301, 20km E Nullarbor homestead; SAMR23005, 125km E SA/WA border; SAMR26171, 13km NE Border Village; SAMR26393, SAMR26395, 12km NW Hughes; Western Australia. SAMR5437, Madura; SAMR23029, 53km E Madura; WAMR91743, 16km SSE Haig; WAMR91831, 28km NNW Middini Beach; WAMR91832, Haig; WAMR91870, 26km ESE Madura; WAMR91924, 19km S Yuwanyandi rock-hole.

DIAGNOSIS

Similar in scalation to *P. barbata*, from which it may be distinguished by the presence of narrow pale transverse stripes on the body, and much more obvious ventral patterning. The tail and limbs are relatively shorter.

DESCRIPTION

Spines and tubercles of the head region very similar to *P. barbata*, including a complete gular scale row, and the occipital and temporal series descending behind the tympanum. Second ceratobranchials absent. Ventral pattern more strongly developed than in other *Pogona*, forming

TABLE 8. Meristic characters of *Pogona nullarbor*.

| Scale Count (n) | Mean (SD) | Range |
|-----------------------|--------------|--------|
| Prenasals (33) | 4.64 (0.70) | 3-6 |
| Subnasals (33) | 3.61 (0.66) | 3-5 |
| Internasals (33) | 11.42 (0.97) | 9-13 |
| Rostral-parietal (32) | 15.63 (1.16) | 13-18 |
| Suborbitals (33) | 3.85 (0.51) | 3-5 |
| Supralabials (32) | 15.53 (1.19) | 13-18 |
| Infralabials (33) | 14.06 (1.09) | 12-16 |
| Mid-body scales (29) | 108.7 (8.45) | 91-125 |
| Lamellae (33) | 20.39 (1.22) | 17-23 |
| Pores (33) | 12.82 (1.69) | 10-16 |

distinctive longitudinal streaks on the gular surface, and the ventral ocellations often coalescing to form irregular streaks on the ventro-lateral surface of the trunk. Preanal and femoral glands active in both sexes. Up to 144mm snout-vent length. Table 8 presents meristic data of the species.

Pogona vitticeps (Ahl, 1926)

Amphibolurus vitticeps Ahl, 1926: 189.

Pogona vitticeps Storr, 1982: 201.

Pogona henrylawsoni Wells & Wellington, 1985: 19.

MATERIAL EXAMINED

New South Wales: AMR15296, Byrock; AMR47319, Wanaaring; AMR59991, AMR59996-7, AMR107409-10, AMR107444, Roto area; NMVD12164, Moona; NMVD52088-9, Broken Hill. Northern Territory: NMVD8970, Plenty River, near Dinkum Mine. Queensland: AM Field tag 11252, 30m WSW Aramac; AMR17122-3, Cunnamulla; AMR107398, Isisford; AMR107406, Aramac; NMVD14181, Dajarrah; NMVD58570, Hammond Downs, near Windorah. South Australia: AMR13904-5, Simpson Desert; AMR21077, Lake Eyre; NMVD1123, Lake Eyre; NMVD3072, NMVR4547-8, Purnong; NMVD41501, Billeroo Creek; NMVD41502, Coolibah Dam; NMVD13781-2, Mulka, via Martee. Victoria: NMVD648, Gawler Ranges(?); NMVD699-700, Raak Plains; NMVD777, NMVD970, NMVD1031, NMVD1036, NMVR4855, Ouyen; NMVD787, Red Cliffs; NMVD7871, Mt Hope; NMVD11753-4, Landraak Plain, near Hattah; NMVD15379, Lindsay Point Station; NMVD15382, Mildura; NMVD18220, 53km S Murrayville; NMVD47858, Millewa South Bore; NMVD52637, 3km NNW Chinaman Well; NMVD52742, Ross's Spring, 23km S Tuttye; NMVD53482, NMVD53827, NMVD53836, NMVD53853, NMVD53907, NMVD53925, NMVD54051, NMVD54070-1, NMVD54123, NMVD54131-2, NMVD54144, NMVD54557, NMVD54749, NMVD54754, NMVD54759-60, NMVD54789, NMVD54790, NMVD55036, NMVD55064, NMVD55251, NMVD55305, NMVD55583, NMVD56741, Chinaman Well area; NMVD58472, NMVD58477, 30km WNW Kiamil; NMVD58501, NMVD58548, NMVD58555, NMVD59448, NMVD59818, Milmed Rock area; NMVD60324-5, NMVD60609, NMVD60694-5, NMVD60708, NMVD60741, NMVD60760, NMVD60762-3, NMVD60768-9, NMVD60778, NMVD60785, NMVD60826-8, NMVD60841, NMVD60854, near Sunset Tank.

DIAGNOSIS

Distinguished by the possession of complete transverse gular scale row and a single lateral scale row. Tail short relative to *P. minor*, about

150% of snout vent length in hatchlings falling to 120% in adults.

DESCRIPTION

Occipital crests approach each other at an angle of about 140° to 150°. Occipital and temporal spine series meet laterally, a little behind the tympanum. There is usually a small gap below this point to a group of spines extending from behind the tympanum. Gular scale row complete, formed by several rows of scales about twice as long as their base width. Laterally the gular scale row becomes single and continues up behind the angle of the mouth to meet the postauricular series and enclose a triangle of relatively smooth scales behind the tympanum. Spines of these series behind the tympanum are about 3 times as long as their base width. At the posterior apex of the triangular series the postauricular fold runs medially to a group of tubercles. Lateral scale row of trunk composed of stout spines in a single row. Nuchal scale ridge usually present (0.91). Ventrals usually keeled (0.76), gulars keeled (0.69), or with a rounded surface, keels becoming less pronounced ontogenetically. Second ceratobranchials present. Up to 247mm snout-vent length. Meristic data are presented in Table 9.

REMARKS

For reasons outlined under *Pogona brevis*, I nominate a neotype for *P. henrylawsoni* at this point: AMR143896, 34.4km N of Barkly Highway via Normanton Road, R. Sadlier, G. Shea 6 Apr 1994. It is a little larger than the lost holotype (145mm snout vent length, versus 130), and has an entire tail, but otherwise agrees well with the description of Wells and Wellington (1985). The gular scale row is poorly developed, the ventrals are very weakly keeled, and the colour pattern matches the description entirely, except that the

TABLE 9. Meristic characters of *Pogona vitticeps*.

| Scale Count (n) | Mean (SD) | Range |
|-----------------------|--------------|---------|
| Prenasals (81) | 4.93 (0.75) | 3-7 |
| Subnasals (81) | 4.38 (0.68) | 3-6 |
| Internasals (81) | 11.09 (1.14) | 8-13 |
| Rostral-parietal (80) | 14.79 (1.59) | 11-20 |
| Suborbitals (81) | 4.37 (0.49) | 4-5 |
| Supralabials (81) | 16.99 (1.12) | 15-20 |
| Infralabials (81) | 15.96 (1.19) | 13-19 |
| Mid-body scales (22) | 140.1 (11.1) | 119-164 |
| Lamellae (80) | 21.78 (1.51) | 18-26 |
| Pores (78) | 14.53 (1.97) | 9-19 |

five dumbbell light marks are placed a little further anteriorly, with the first over the axilla, rather than the last over the groin. The locality is about 100km west of the original type locality, but this specimen came nearest to meeting the requirements of the code for nomination of neotypes. The new type locality is also in 'black soil' country specified by Wells and Wellington as the habitat of *P. henrylawsoni*.

MORPHOLOGICAL VARIATION

Storr (1982) claimed *Pogona* was distinguishable from *Ctenophorus* by 'alignment of pre-anal pores backwards towards the midline'. In fact this feature is common in only *P. minor minima* and *P. m. minor* from the adjacent mainland. Storr's diagnosis, strictly applied, would exclude all species assigned to the genus except some *P. minor*. The preanal pores of some *P. m. mitchelli* (e.g. AMR101470, WAMR45759) are more or less parallel with the vent, and in a separate series from the femoral pores. However, the arrangement of pores in other *Pogona*, including most *P. m. mitchelli*, is more or less identical to that found in *Ctenophorus nuchalis*, the feature used by Storr (1966) to distinguish between it and the otherwise very similar *C. reticulatus*.

The pore arrangement in some *P. m. minima* deserves special comment. Within this small island population the full range of variation in pore arrangement can be found. Individuals vary from the 'nuchalis' pattern (WAMR19506) through to an arrangement very similar to that found in *Amphibolurus* (WAMR19505) (Fig. 3).

The dentition of all *Pogona* is similar. Hatchlings have a single median 'egg' tooth. This is followed by a small tooth on either side of the premaxilla, and then a central tooth erupts. Premaxillary teeth are usually considered pleurodont (Cooper et al., 1970), as are the most anterior teeth on both the maxilla and dentary in adults. The anterior dentary and maxillary teeth are caniniform, resembling the canines of carnivorous mammals. These teeth are also absent in hatchlings, appearing later in development. The attachment to the bone tends to be slightly lateral to the line of the acrodon teeth row. In skeletal material they are embedded within the bone, and successional may be a better descriptor than pleurodont. In adults the anterior successional teeth interlock when the mouth is closed. The most anterior dentary tooth passes into the gap between the median and lateral premaxillary tooth. More posterior teeth continue this meshing, but the arrangement is sometimes irregular.



FIG. 3. Variation of pore arrangement in specimens of *P. minor minima*. Note the variation from a '*Ctenophorus nuchalis*' arrangement in WAMR19506 to an '*Amphibolurus*' arrangement in WAMR19505.

Successional teeth are replaced by larger teeth during growth. This is apparent in some specimens, where more than the usual number of teeth are present, and the 'bite' may be temporarily unorthodox.

The tympanum in *Pogona* is below the level of the surrounding skin, at the bottom of a short meatus. The tympanum is ontogenetically further concealed by the development of a skin fold over the postero-superior part of the tympanum. This fold is small in hatchlings, at first flattening the postero-superior margin of the tympanic opening to make it roughly triangular. As the animal grows, more of the tympanum is covered. In some adults more than half the tympanum is covered, and the 'ear' aperture is oval and much smaller than the contained tympanum.

The occipital crest in most species closely approaches or joins the temporal spine series laterally so that the posterior part of the head is surrounded by a triangular series of spines. This is prominent in *P. vitticeps* and *P. m. mitchelli*, and in these taxa there is usually a gap between

the corner of the triangle and the postauricular spines. The arrangement is similar, but less prominent in other *P. minor* and in *P. microlepidota* and *P. brevis*. In the latter two species the occipital series does not usually join the temporal series. In *P. barbata* and *P. nullarbor* the occipital and temporal series continue down behind the tympanum in parallel series. Variations in these spine arrangements were the main features used to distinguish species in Badham's (1976) revision of the genus.

The labial scales in most *Pogona* are smooth, but most *P. m. minima* have labial scales with a longitudinal ridge. This feature is also present in many mainland *P. minor* of both other subspecies, and in all *P. minor* the ridge tends to be better developed in the supralabial series. Some *P. microlepidota* have a faint ridge on the supralabial scales, and some small *P. nullarbor* specimens also had some indication of a ridge on the supralabials. Otherwise the character is confined to the subspecies of *P. minor*.

One feature distinguishing *Pogona* from most other Australian agamids is the presence of a row of spines on the paramarginal scales of the lower eyelid. This row of spines is shared with the burrowing *Ctenophorus* of the *C. reticulatus* species group (Witten, 1982b). The spines of this row become more prominent ontogenetically, the best developed spines appearing in the largest specimens. This correlation with size crosses species boundaries to some extent. Very small *C. clayi* (the smallest species with the feature), for example, having only rudimentary spines (Witten, 1982a). Within *Pogona* there is some variation apart from that expected from size. The spines are less well developed in *P. vitticeps*, particularly from the south of its range. The smaller animals from the Big Desert (Witten & Coventry, 1990) have weaker spines than *P. m. minor* of comparable size. *P. m. minor* from the Western Australian coast and *P. m. minima* also have less well-developed spines, with some adult specimens having little more than triangular ridges on the paramarginal scales.

Most Australian agamids have subdigital lamellae which are smooth centrally with a lateral projection on either side. All *Pogona* species have individuals with this condition. A common variation includes the distal few lamellae having four ventral projections rather than two. This condition is particularly common in *P. m. michelli*, with more specimens having four spines than two. Some specimens of all *Pogona*

taxa exhibit variation in the number of spines on the subdigital lamellae.

All living *Pogona* I examined had some indication of yellow pigmentation in the mouth lining. This is variable, and Bradshaw (1970) commented that northern populations of *P. m. minor* had a white lining, while southern populations had the more typical yellow pigmentation. I have not examined living specimens of *P. microlepidota*.

The glands secreting through the preanal and femoral pores are subject to some sexual dimorphism in *Pogona*. *P. minor* may be sexed with reasonable reliability by the differential enlargement of the pores in males. The pores in females are not increased in relative size from hatchlings (0.1–0.2 mm), but in males are obviously more active and enlarged (0.4–0.65 mm). The same is not true of other species of the genus. In *P. nullarbor* pores are of a similar size in both sexes, and are clearly actively secreting at a similar level. In other species pores are more variable in size, usually more active in males, but the sex difference seen in *P. minor* is not as pronounced.

The colour of *Pogona* has often been described as reddish or brown, as well as the more common grey. All species with which I am familiar are patterned in shades of grey, with the single exception that there is often a small orange flash beneath the tympanum. Animals which are in the process of shedding their skin often have a distinct contrast between the old and new skin. Apparently the 'old' skin becomes dusty, picking up local soil to allow better colour matching with their normal background. Most animals which appear to be brown or red are probably from areas with soil of that colour.

DISCUSSION

Pogona minor is a wide-ranging species containing three main morphs. These were considered as separate species by Badham (1976), but were reduced to subspecies by Storr (1982), who also redefined the boundary between *P. minor minor* and *P. m. minima*. Badham referred specimens from the south west corner of the continent to *P. minima*, while Storr restricted *P. m. minima* to the type locality of the holotype (Houtman Abrolhos Islands). There is merit in both boundaries. Storr is clearly correct in reducing *P. minima* to subspecific rank. The population on the Houtman Abrolhos closely resembles morphologically *Pogona* on the adjacent mainland. This mainland population intergrades into typical

P. m. minor as the climate becomes increasingly arid moving both north and east from the south west corner. Meristic features do little to resolve whether Badham's or Storr's boundary should be preferred (Table 6). Mainland *P. 'minima'* are generally intermediate between Houtman Abrolhos and central Australian animals. However, in the number of lamellae under the fourth toe the mainland '*minima*' morphs have a lower count than either eastern *P. m. minor* or typical *P. m. minima*. This may have influenced Storr in nominating subdigital lamellae as an important diagnostic feature separating *P. m. minor* from *P. m. minima*, particularly because he examined almost exclusively Western Australian specimens (7 specimens from N.T., 4 from S.A.). Morphometric data show a much clearer separation between mainland '*minima*' morphs and typical *P. m. minima* (Witten, 1994), there being little morphometric difference between mainland '*minima*' and *P. m. minor*. Even morphometric data, however, will only allow the separation of most specimens. The presence of this east-west cline within *P. minor* demonstrates continuing gene flow between the different populations. The recognition of *minima* as a race might be more appropriate. I would prefer to leave the nomenclature as stable as possible, and the present status of this taxon is at least defensible, given geographic isolation of the most westerly animals.

There is a second cline within *P. minor*. Apart from the east-west cline towards *P. m. minima* in the west, there is a north-south cline with *P. m. mitchelli* in the north. The distinction between these subspecies is much better defined. Storr (1982) had more specimens than Badham (1976), and was better able to define the boundary between *P. m. minor* and *P. m. mitchelli*, having first recognised that *mitchelli* represented a subspecies of *P. minor*. Four paratypes of *Amphibolurus mitchelli* should be considered *P. m. minor*. Two of these, WAM20078-9 from Tambrey, Storr reassigned to *P. m. minor* without comment. They are simply listed among specimens examined. The tags on these specimens, incidentally, do not have the normal 'R' prefix on other reptile specimens in the Western Australian Museum. Two South Australian Museum specimens, also from Tambrey or near it (SAMR4484 is from Kangiangi), were listed as paratypes of *A. mitchelli* (Badham, 1976). One, SAMR4483, I identified as *P. m. minor* not realising at the time that it was a type of *A. mitchelli*. The other specimen, SAMR4484,

examined as a series of *P. m. mitchelli*, has its occipital crest on a raised skin fold. My notes on the specimen included the comment 'nearer *minor* than *mitchelli*'. All four of these specimens have occipital crests of relatively small spines. All are sexually mature with wide heads, but no wider than typical *P. m. minor*.

Three specimens of *P. nullarbor* are quite different (SAMR23939-41). Normal *P. nullarbor* have an arrangement of the occipital and temporal spines similar to *P. barbata*, but these animals closely resemble *P. m. mitchelli* in these features. They also have a single lateral series of spines. They are identifiable as *P. nullarbor* because they have a complete gular scale row, and the strongly developed ventral pattern is also characteristic of *P. nullarbor*. These specimens were all hatchlings from a clutch laid in captivity by SAMR18581, reported by Smith & Schwaner (1981). Other hatchlings from the same clutch (SAMR19807, SAMR20106, SAMR25298-301) were typical *P. nullarbor*. All of these specimens were kept in captivity for varying periods. It is possible that the conditions under which they were kept influenced their morphology.

PHYLOGENY

P. brevis appears to be the most primitive member of the genus, if only because it is least divergent from the presumed ancestor of the genus, a species resembling *Ctenophorus nuchalis*. The 'farriers rasp' condition of the dorsal scales is least developed in *P. brevis*, and its short appendages and rounded head resemble *C. nuchalis*. Its relationship to other species of the genus is unclear.

P. minor might be nearest the main stock of *Pogona*, a widespread variable species with several morphs. It appears some of these morphs have become fixed and evolved into distinct species. *P. vitticeps* is very close to *P. m. mitchelli* in morphology, differing mainly in the possession of a 'beard' and larger adult size. The Pleistocene Lake Dieri may have acted as an isolating mechanism between *P. m. mitchelli* in the west and *P. vitticeps* in the east in the way suggested by Pianka (1972) for other arid adapted lizards.

P. microlepidota appears to be a northern isolate derived from *P. minor mitchelli*. The two taxa are similar in most features, *P. microlepidota* being distinguished mainly by the very strongly keeled ventrals and a multiple lateral scale row. The lateral scale row similarity to *P. barbata* is puzzling, *P. microlepidota* is a little larger (maximum SVL 180mm; Storr, 1982) than *P. m.*

mitchelli (171mm) which is in turn larger than *P. m. minor* (145mm; Badham, 1976). These taxa thus parallel the situation in *P. vitticeps*, where southern populations are smaller (Witten & Coventry, 1990).

P. barbata is so similar in size to *P. vitticeps* it is easy to think of them as being close phylogenetically. However, *P. barbata* is the most derived member within the genus, having lost the second ceratobranchial (Badham, 1976) and its likely ancestry is unclear. *P. nullarbor* is apparently related, having also lost this hyoid element (Badham, 1976), and may represent a western isolate of *P. barbata*. The smaller size of *P. nullarbor* may be a further example of southern taxa being smaller than northern forms as discussed above. However, because *P. nullarbor* is nearer the presumed ancestral form in size, I favour the idea that *P. barbata* is an eastern derivative of *P. nullarbor* rather than the reverse. Another factor to consider is that *P. barbata* and *P. nullarbor* share the character of a multiple lateral scale row with *P. microlepidota*. This may indicate phylogenetic relationship, but three captive specimens of *P. nullarbor* which developed a single lateral scale row (see above) discourages heavy reliance on this feature. A complete gular scale row is a feature shared by *P. barbata*, *P. nullarbor* and *P. vitticeps*. Again this may indicate common ancestry, but is not a strong character. At our present state of knowledge the relationship of *P. barbata* and *P. nullarbor* to other members of the genus is unclear.

Pogona is clearly related to *Ctenophorus nuchalis*. The genus shares with this species the derived characters of a novel arrangement of preanal and femoral glands, a series of spines on the lower eyelid, and a narrow premaxilla (Witten, 1982b). The presence of these derived characters led me earlier to abandon *Pogona* as potentially ancestral to other Australian agamids. Variation within *P. minor* indicates this was an error. *P. m. minima* is more arboreal than the other subspecies, and has characteristics suggesting it may share a recent common ancestor with the *Amphibolurus* radiation (including *Lophognathus*, *Diporiphora* and *Caimunops*).

Members of the *Amphibolurus* radiation differ from *Pogona* in a number of features. They retain the presumed primitive characters of a ridge rather than spines on the paramarginal scales of the lower eyelid and a relatively wide premaxilla. The derived features which characterise *Pogona* are all less pronounced in *P. m. minima* than in other *Pogona*. The spines on the lower eyelid are

less well developed than in other taxa of *Pogona*, and some specimens approach the primitive condition where the paramarginal scales of the eyelid possess a simple ridge. The number of pleurodont teeth in *P. m. minima* is also higher at a smaller size than in *P. m. minor*, at least for dentary teeth (mean = 4.82 ± 0.75 , $n = 11$; *P. m. minor* mean = 3.44 ± 1.05 , $n = 91$). If this character is part of the selective trend towards *Amphibolurus* then the slightly broader premaxilla of the *Amphibolurus* radiation is a logical outcome of further selection.

Derived features characterising the *Amphibolurus* radiation include the possession of ridged labials and a peculiar pore arrangement. *P. minor* from far western continental Australia frequently have ridged labials, and *P. m. minima* usually have at least weakly ridged labials. The *Amphibolurus* pore arrangement is characterised by the preanal pores presenting in a postero-medial series more closely spaced than the femoral pores. This arrangement is found in some *P. m. minima* (Fig. 3) and *P. m. minor* from the adjacent mainland.

Chlamydosaurus is one of the most bizarre lizards of the world and its relationships have never been clear. Cogger (1961) included it in the *Amphibolurus* radiation, and this has been accepted in other accounts of agamid relationships (Witten, 1982a; Greer, 1989), largely on the basis of the shared pore arrangement. It lacks several of the features characteristic of the *Amphibolurus* radiation. The labials in *Chlamydosaurus* are smooth, the premaxilla is narrow, and the pore arrangement is less regular than in other members of the *Amphibolurus* radiation. A separate derivation of *Chlamydosaurus* from within *Pogona* would explain these differences. Within *Pogona* only *P. minor* from south west Australia and *P. m. minima* commonly have ridged labials, and all *Pogona* have a narrow premaxilla with 3 premaxillary teeth the maximum. The arrangement of pores in *Chlamydosaurus* is variable, and a selection of the variations in Fig. 3 could serve to illustrate the normal variation in *Chlamydosaurus*, indicating that the variation now seen in *P. m. minima* may have been shared by the original stock which gave rise to *Chlamydosaurus*.

The observed variation in *P. minor* is very interesting in the context of Australian agamid phylogeny. The pore arrangement of some *P. m. minima* closely resembles that found in *Amphibolurus* and other closely related genera. Given several other features shared by *Pogona* and *Amphibolurus*, there seems little doubt that

the *Amphibolurus* radiation arose from stock which also produced *P. m. minima*. It is remarkable that the character which typifies the *Amphibolurus* radiation more than any other should persist in a subspecies of its presumed ancestor. That several other features, such as the horizontally ridged labials, are also present in *P. m. minima* is perhaps even more remarkable. There are two possible explanations.

It is possible that the suite of characters found in the *Amphibolurus* radiation is at least originally an adaptation to more mesic conditions. The present distribution of these characters within *P. minor* may be the result of selection in the more mesic coastal parts of south western Australia. While the benefit of the derived features seen in *Amphibolurus* are unclear, it is certainly possible that they confer advantages on the coastal populations not shared by populations in arid areas. Under this hypothesis a stable cline may persist for very long periods. There has apparently not been any substantial barrier to continuous gene flow in western Australia between arid- and mesic-adapted populations.

Some indication of the period over which this cline has remained stable is given by the biochemical work of Baverstock and Donnellan (1990). Extrapolating from their figure of relationships based on differences in albumins a separation time of about 7 million years between *Pogona* and the *Amphibolurus* radiation is indicated. Given the variable rates demonstrable in albumin evolutionary rates among other agamids (Joger, 1991) this figure may need to be revised. However, the variation within the presumed derivatives of the ancestor of *Pogona minor* indicate that this is indeed an ancient cline.

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RELATIVE GROWTH IN *POGONA* (REPTILIA: LACERTILIA: AGAMIDAE)

G.J. WITTEN

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The growth of a group of captive-bred *Pogona brevis* was studied over a period of a year. The data collected from these individuals were compared with data from other species of the genus, and two species from closely related genera. *P. brevis* has a shorter tail and limbs than other members of the genus. *P. minor* has three subspecies which differ from each other to a similar extent as most other species. In the case of *P. minor minima* this probably reflects adaptation to a different ecological niche. Mainland specimens placed in *P. m. minima* by Badham (1976) because of morphological similarities were indistinguishable from other *P. m. minor* morphometrically. The intraspecific variation within *P. minor* helps confirm the long maintenance of an East-West cline in the species. Enough data from *P. minor* and *P. vitticeps* were collected to analyse growth changes after sexual maturity was attained. For some measurements there were distinct changes in relative growth rates at maturity while others changed little. There were differences between the two species in which proportions were affected. These differences affect correlation coefficients, and it was unclear whether data collected from a small group of individuals over time were better indicators of relative growth patterns than data from museum specimens from scattered localities. All species within the genus differ morphometrically in some features. Morphometric data have proved useful in taxonomic decisions from intergeneric to subspecific levels. □ *Reptilia, Agamidae, Pogona, relative growth, morphometrics.*

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Many contributions to agamid taxonomy have employed body proportions. Earlier contributions used simple arithmetic proportions (e.g. Storr, 1966), but Badham (1976) employed allometric data of tail length to help distinguish between *P. barbata* and *P. vitticeps*. Witten (1985) compared relative growth of a large number of agamid lizards, and found phylogenetic relationships at the generic level were supported by allometric data. Johnston (1992) used allometric analyses to help distinguish *Ctenophorus tjantjalka* from closely related species.

Three features of allometric change have been suggested as significant indicators of evolutionary relationships. Huxley (1932) suggested that allometric coefficients might act as important phylogenetic indicators; Gould (1977) emphasised the conservatism of early development, and considered juvenile proportions were better phylogenetic indicators; Dodson (1975) thought that ecological constraints would influence relative growth, particularly in animals lacking parental care.

The work by Witten (1985) certainly provided support for Gould; related species were more similar in body proportions as juveniles than as adults. These data provide less support for

Huxley's suggestion of similar allometric coefficients in related species. The lack of detailed ecological work means that Dodson's hypothesis remains effectively untested. Witten's study was preliminary. Most data came from museum specimens, and for most species data were compiled from animals collected over a wide area, from different populations. Allometric data for some species were based on as few as 12 specimens, and the analyses were thus limited to rather crude estimates. This was enough to allow broad comparisons to be drawn, and to infer taxonomic and phylogenetic relationships, particularly at higher levels. In the absence of a greater data base it has been difficult to assess whether the inferences drawn by Witten were justified.

Melbourne Zoo recently (1990) bred a clutch of downs bearded dragons (*Pogona brevis*). These animals presented the opportunity to gather data from a series of closely related specimens over a growth period. As part of a taxonomic revision of the genus data were collected for the other species in the genus, largely from museum specimens using methods similar to Witten (1985). An assessment of the methodology used by Witten (1985) is therefore possible. The enlarged data base also allows an extension

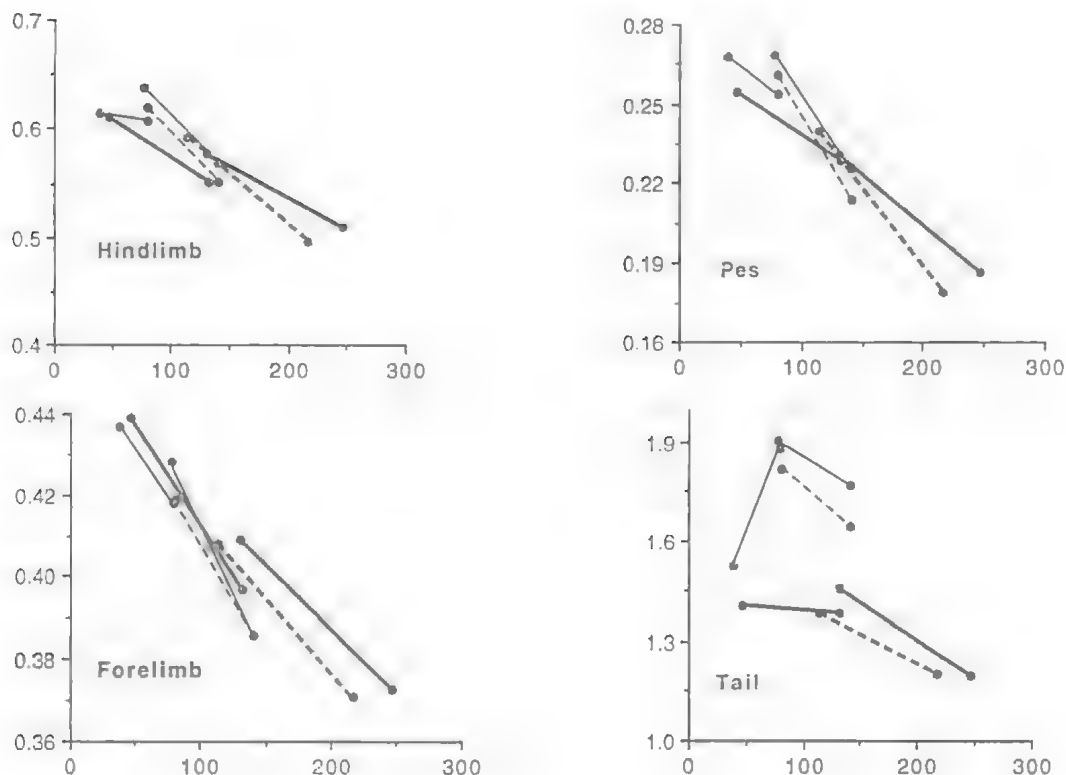


FIG. 1. Relative lengths of appendages in *P. minor* and *P. vitticeps* showing changes at sexual maturity. Male and juvenile data represented by unbroken lines, females by broken lines. The lines extend over the observed size range for each category. *P. vitticeps* grow larger, and are represented by thicker lines. All measurements are plotted as ratios of the snout-vent length against snout-vent length, to emphasise the changing ratios, but each line is calculated from the least squares regression of logged data.

of the use of allometric data. A number of issues need to be addressed: 1, Witten (1985) made no attempt to examine possible sexual dimorphism and how this related to allometric changes. The large amount of data collected from *Pogona minor* allow this area to be explored; 2, previously animals from different localities and possibly different populations were used to calculate relative growth of species. This can now be compared to data collected from siblings during growth, and the validity of lumping data from several populations may be assessed; 3, allometric data from a congeneric group of species could be compared with the broad approach taken by Witten (1985). He found differences useful in separating generic level groups, but closely related

species showed less variation in allometry. Recent work has confirmed the phylogenetic position of *Pogona* between *Ctenophorus* and *Amphibolurus* (Witten, 1994), so comparisons with *Ctenophorus nuchalis* and *Amphibolurus norrisi* were made to examine the generic definitions. The variety of taxa within and near *Pogona* now allow comparisons between subspecies, closely related species, congeners not closely related, as well as species from closely related genera. This should allow an assessment of the utility of relative growth data in taxonomic and phylogenetic studies.

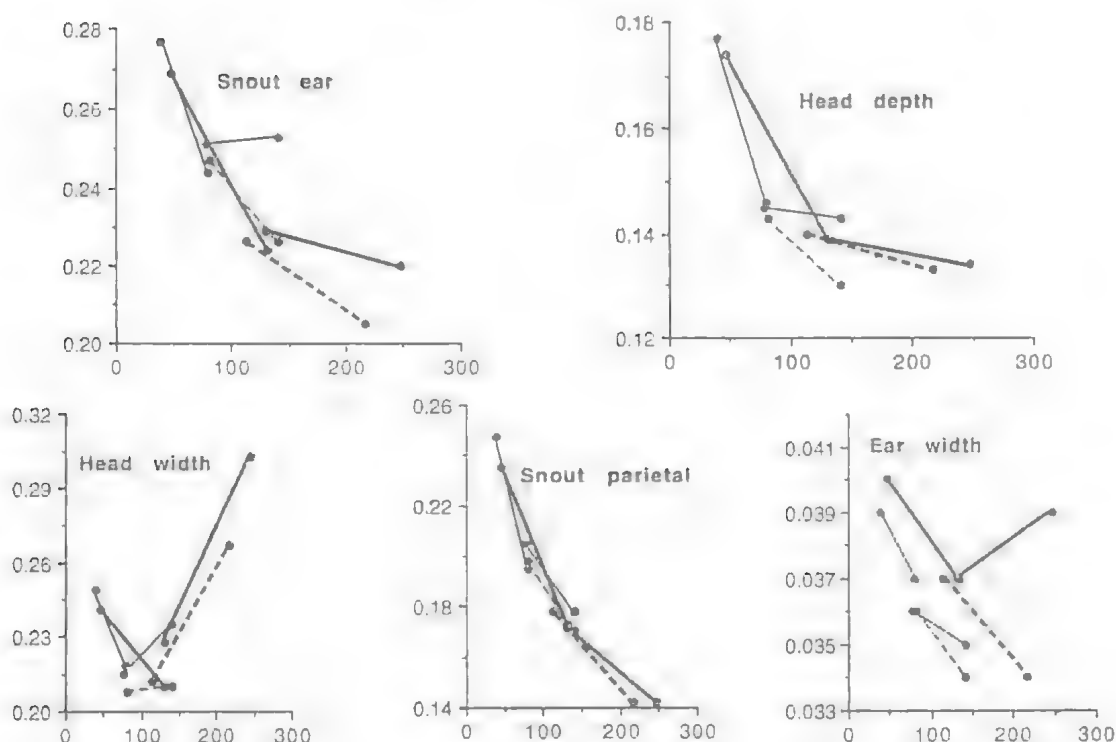


FIG. 2. Head proportions of *P. minor* and *P. vitticeps* to show changes at sexual maturity. Lines as for Fig. 1.

MATERIALS AND METHODS

Limb, tail and snout vent lengths were measured to the nearest 0.5mm using a perspex mounted ruler. Other measurements were recorded using dial calipers accurate to 0.05mm. Where possible, measurements were recorded on both sides of the body and the mean used in analyses. Head depth was recorded at the centre of the orbit. Pes length was taken as the distance from the base of the claw on the fourth toe to the furthest point of the tarsus with the ankle fully flexed. Morphometric data were analysed as in Witten and Coventry (1990), with logged data regressed by the least squares method to calculate Huxley's allometric formula. The calculated regression lines were used to illustrate allometric changes over the observed size range for each taxon, although the data were converted to ratios of snout vent length in figures to emphasise differences between groups of data.

RESULTS

INTRASPECIFIC COMPARISONS

The large amount of data collected to compare mainland '*minima*' morphs with typical *P. m. minor*

and *P. minor minima* (see below) allowed a more detailed analysis of growth. The sex of all adult *P. minor* is easy to tell by the activity of the preanal and femoral glands, with males having more active glands and consequently wider pores with more secretion (Witten, 1994). Animals of adult size were sexed as they were measured, mainly by examination of gonads, but also by examination of pores where the abdominal cavity was not open, and the morphometric data analysed for both sexes. Smaller animals were treated as a single class to give a growth calculation up to the size at which sexual maturity is normally attained. Data for *P. vitticeps* collected to establish the taxonomic status of smaller specimens from the Victorian mallee (Witten & Coventry, 1990) allowed similar analyses to be carried out for that species. There were insufficient data for the other species to be analysed in this way.

In most measurements there is a shift in the rate of allometry at sexual maturity (Figs 1, 2). The single exception is forelimb length (Fig. 1), where there is little change, and there is little sexual dimorphism. For the hindlimb and pes data, the negative allometry characteristic of the genus in these meas-

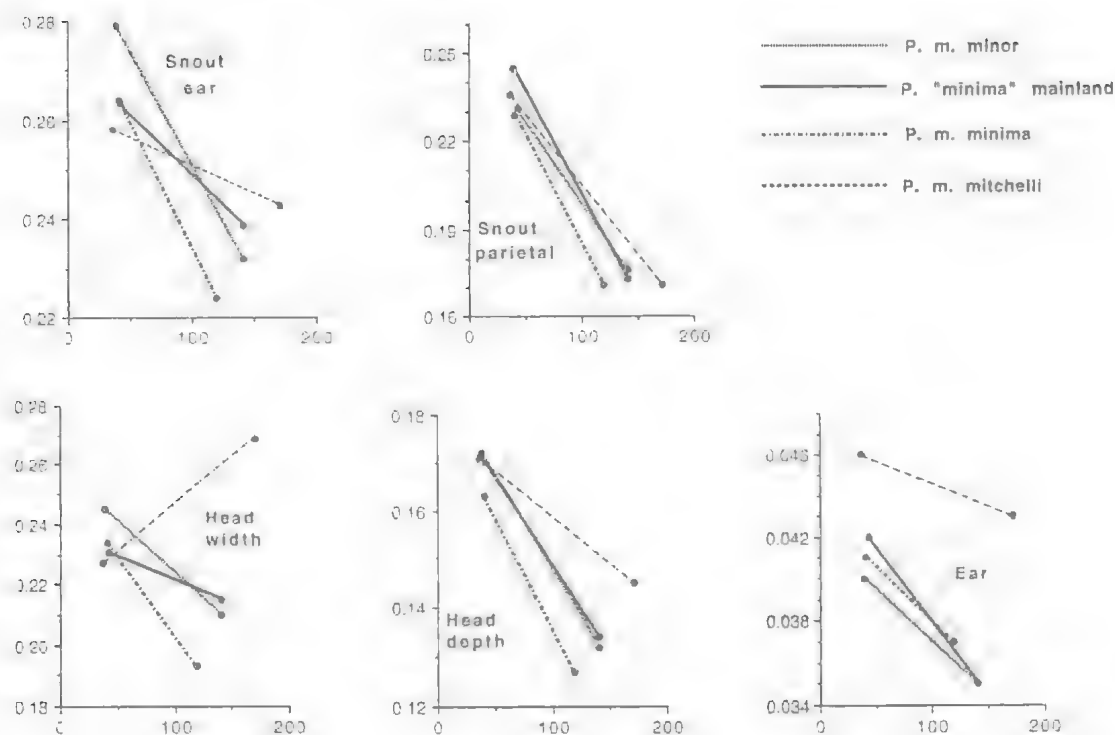


FIG. 3. Head morphometric data of *P. minor*. Each line represents the least squares regression line over the recorded size range for each population or subspecies, but converted to ratios as in Fig. 1.

urements accelerates at sexual maturity for *P. minor*, although this is not pronounced in *P. vitticeps*. Tail length in *P. minor* increases rapidly during juvenile growth, but decreases in both sexes after sexual maturity. Males have relatively longer tails, but this is apparently achieved during early growth, and is simply maintained after sexual maturity (Fig. 1).

All head measurements show negative allometry during growth, as is typical of vertebrates (Gould, 1977). At sexual maturity, however, this trend is at least slowed. In male *P. minor* there is positive allometry of head width and the snout-ear interval after maturity, suggesting a larger head not present in females (Fig. 2). In *P. vitticeps* ear width increases after maturity in males, but not females, and both sexes have strong positive allometry of head width (Fig. 2). In both species juvenile negative allometry for the snout-parietal interval and head depth is slowed, but there is little sexual dimorphism.

Large males of most Australian agamids develop 'jowls', an expansion around the posterior

part of the head. The positive allometry of head width is therefore not unexpected for male *P. minor*. *P. vitticeps* are characterised by a wide head, and the positive allometry of both sexes in this species is also unremarkable. What is not immediately apparent from casual observation is that males tend to have larger heads overall than females, particularly in *P. minor*. The length, as indicated by the snout-ear measurement, and the depth of the head, are greater in larger males than females of similar size (Fig. 2). With this additional data it is apparent that head width is not dissimilar to other head measurements, and 'jowls' may not have influenced head width measurements significantly. The wider ear aperture of male *P. vitticeps* was also not detected in other analyses, nor is it obvious from casual observation.

SUBSPECIFIC COMPARISONS

Pogona minor was originally described as a subspecies of *P. barbata* (Sternfeld, 1919), as was *P. minima* (Loveridge, 1933). Badham (1976) treated both as full species, and described the related *P. mitchelli*. Storr (1982) reduced the latter two taxa to

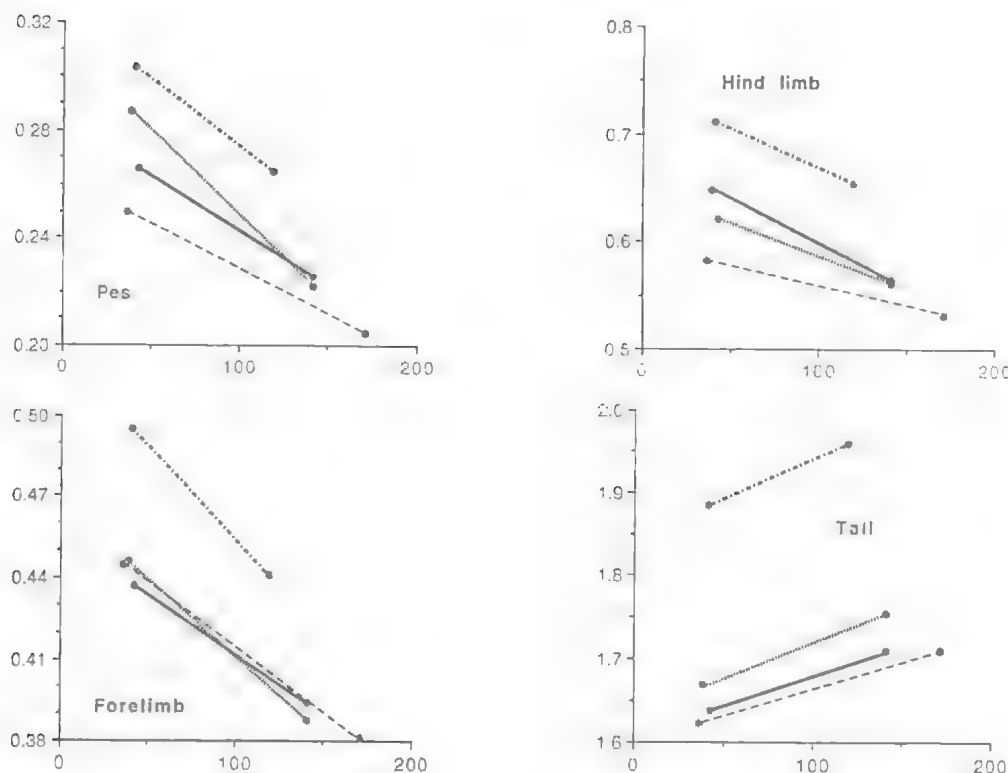


FIG. 4. Appendage morphometric data of *P. minor*. Lines as for Fig. 3.

subspecies of *P. minor*. Storr also restricted *P. m. minima* to the type locality of the holotype, the Houtman Abrolhos Islands. Originally *P. m. minima* included some specimens from the mainland adjacent to the Houtman Abrolhos, and Badham had assigned *Pogona* from the south west corner of Western Australia to *P. minima*.

Badham (1976) used the presence of a 'distinct nuchal row of 5 or 6 spines parallel to and on either side of the vertebral column' as the main feature characterising *P. minima*. Using this character, I sorted mainland specimens into 'minima' morphs and *P. m. minor*. Animals intermediate in morphology or distribution (following Badham's boundaries between the taxa) were excluded from these analyses.

Analyses of the resulting morphometric data indicate that mainland 'minima' morphs are much nearer *P. minor* than *P. m. minima*. *P. m. mitchelli* diverges strongly from the other populations in the possession of a much wider head, as

originally described by Badham (1976), and also has a slightly deeper head at its maximum size than other *P. minor* (Fig. 3). The width of the ear opening is wider in *P. m. mitchelli* at all sizes. *P. m. minima* differs from other *P. minor* in developing a slightly smaller head, best illustrated in the snout-ear and head width measurements. *P. m. minima* differs from other *P. minor* more markedly in the length of its appendages (Fig. 4), with longer tail, hind limb and forelimb at all sizes. *P. m. mitchelli* tends to have a shorter hind limb than both the 'minima' morphs and typical *P. minor*, but is similar in tail and forelimb length (Fig. 4).

SPECIES COMPARISONS

Head width data show some dramatic differences between taxa. There are considerable differences in the relative head widths of juveniles, but the remarkable data are in the development of relatively wide heads in the adults of some taxa. *P. vitticeps*, as suggested by its specific name has

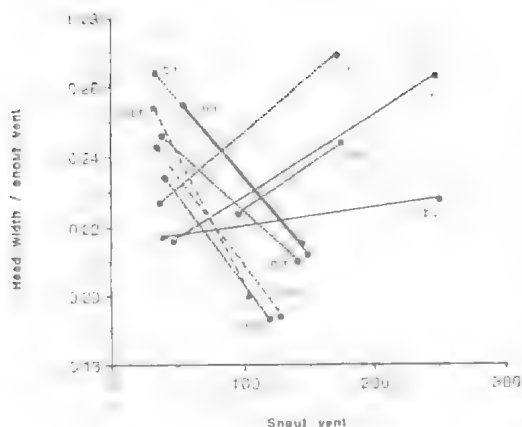


FIG. 5. Head width data for *Pogona*. Lines drawn as for Fig. 1. Unbroken lines: ba = *P. barbata*; br = *P. brevis*; mc = *P. microlepidota*; mr = *P. m. minor*; ma = *P. m. minima*; mt = *P. m. mitchelli*; nul = *P. nullarbor*; vi = *P. vitticeps*. Broken lines: nor = *Amphibolurus norrisi*; nuc = *Ctenophorus nuchalis*.

a very wide head, achieved through strong positive allometry of head width (Fig. 5). However, *P. m. mitchelli* has a relatively wider head than *P. vitticeps*, and *P. microlepidota* is similar to *P. vitticeps* in both relative head width and in the allometric changes. The other 'giant' *Pogona*, *P. barbata*, maintains a relatively wide head throughout growth, in contrast to the negative allometry of all other taxa (Fig. 5).

Head depth is similar in juveniles of all species studied, but becomes relatively deeper in *P. m. mitchelli* and *P. microlepidota* (Fig. 6). Remarkably little variation occurs in the other head measurements. For snout-parietal (Fig. 7) and snout-ear (Fig. 8) distances most *Pogona* achieve similar adult ratios, although at a much larger size in *P. vitticeps* and *P. barbata*. *P. brevis* differs in the juvenile ratios of both these measurements, but this may be an artefact of having data from very small specimens (see Discussion).

P. m. minor, *P. m. minima* and *P. vitticeps* have a narrower ear aperture than other *Pogona* (Fig. 9). Other taxa, including *P. m. mitchelli*, have higher ear width measurements. *P. nullarbor* is the only species with marked allometry in this measurement, strong negative allometry taking it from the 'wide ear' group as a juvenile to the 'narrow ear' group as an adult.

Hind limb length decreases with growth in all species measured. There are some large dif-

ferences within *P. minor*. *P. m. mitchelli* has the shortest hindlimb of all taxa measured, while *P. m. minima* has longer hind limbs than all but *P. microlepidota* (Fig. 10). The results for the last species need to be treated with caution, as there were very few specimens available for study. Of the other taxa in *Pogona*, there is more variation among the juvenile measurements than those at larger sizes, with *P. brevis* having the second longest hind limbs as hatchlings after *P. m. minima*. *P. nullarbor* and *P. brevis* have stronger negative allometry than other *Pogona*.

The pes length contributes to the total hind limb measurement, and not surprisingly analyses of pes length parallel those for the hind limb (Fig. 11). *P. m. minima* and *P. microlepidota* are again above the main group of *Pogona*. *P. brevis* and *P. nullarbor* have a relatively shorter pes at their maximum size.

P. m. minima and *P. microlepidota*, both outstanding because of high hind limb and pes measurements, also have longer forelimbs than other *Pogona* (Fig. 12). *P. brevis* has longer forelimbs as juveniles, but at adult size falls within the main group. Only *P. nullarbor*, with slightly shorter adult forelimbs varies from this main group of *Pogona* species (Fig. 12).

Variation in tail length within *Pogona* allows the genus to be split into three. No species has strong allometry, but *P. brevis* has a much shorter tail throughout its size range (Fig. 13). *P. nullarbor*, *P. vitticeps* and *P. barbata* form an intermediate group, while the subspecies of

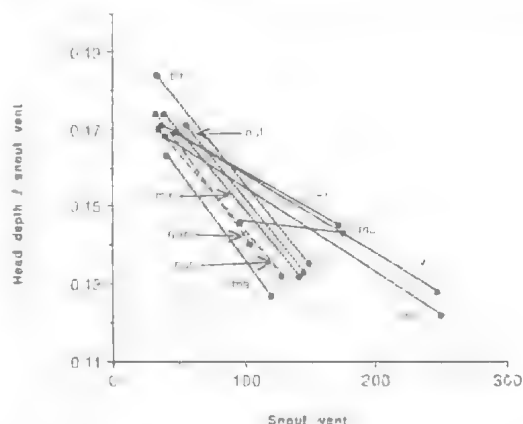


FIG. 6. Head depth data for *Pogona*. Lines and abbreviations as for Fig. 5.

TABLE 1. Correlation coefficients (r^2) for regression calculations of three species of *Pogona*.

| Measurement | <i>P. brevis</i> ($n=86$) | <i>P. minor</i> ($n=86$) | <i>P. vitticeps</i> ($n=70$) |
|----------------|--------------------------------|-------------------------------|-----------------------------------|
| Head width | 0.988 | 0.960 | 0.973 |
| Snout parietal | 0.984 | 0.977 | 0.987 |
| Snout ear | 0.993 | 0.976 | 0.989 |
| Head depth | 0.983 | 0.965 | 0.984 |
| Ear width | 0.958 | 0.873 | 0.954 |
| Tail length | 0.985 | 0.949 | 0.977 |
| Hind limb | 0.987 | 0.979 | 0.992 |
| Pes length | 0.978 | 0.962 | 0.980 |
| Forelimb | 0.990 | 0.986 | 0.991 |

P. minor and *P. microlepidota* form a third group with longer tails (Fig. 13).

INTERGENERIC COMPARISONS

Both species included for comparison with *Pogona* resemble *P. m. minima* in head width. As juveniles both *Amphibolurus norrisi* and *Ctenophorus nuchalis* have slightly wider heads, but have relatively narrower heads than all *Pogona* as adults (Fig. 5). For head width the two non-*Pogona* species fall within the range of typical *Pogona*, differing only from those *Pogona* species with larger heads. In head length, however, *A. norrisi* has a longer snout-ear interval than most *Pogona*, while *C. nuchalis* develops a shorter snout-ear interval during growth (Fig. 8). This difference is not as apparent in the snout-parietal measurement, but the same trend is present (Fig. 7).

The ear width measurements reflect the development in *Pogona* of a sunken tympanum. *Ctenophorus nuchalis* has a superficial tympanum which is probably not significantly smaller than the tympanum in *Pogona*, but the ear width measurement in the latter is really a measure of the size of the opening to the auditory meatus, not a measure of the tympanum itself. *Amphibolurus norrisi* retains the sunken tympanum of *Pogona*, and differs little in this measurement (Fig. 9).

Amphibolurus norrisi has very long hind limbs, including the pes, relative to most *Pogona*, but relatively short forelimbs. *Ctenophorus nuchalis*, however, is nested among the 'typical' *Pogona* for all limb measurements (Figs 10-12). Similarly, the tail is long in *A. norrisi*, but the tail of *C. nuchalis* is shorter than all *Pogona* but *P. brevis*.

SAMPLE COMPARISONS

The measurement of a clutch of lizards over a growth period provided a large amount of data from a small sample of closely related animals. This is a strong contrast with the data of Witten (1985), and for the data from other species in this study.

Data from a similar number of *P. minor* were compared with the data from *P. brevis*. Most of the *P. minor* data were taken from South Australian specimens, and an attempt was made to use specimens of a similar size distribution. The correlation coefficients from the two sets of data were compared (Table 1). As might be expected, the *P. brevis* data had higher correlation coefficients than the data from *P. minor*. Data from 70 *P. vitticeps* were also compared with the other sets of data. These data, like those from *P. minor*, came from specimens from a wide area, but unlike the *P. minor* data, had correlation coefficients higher than the *P. brevis* data for some measurements (Table 1).

The comparatively high correlation coefficients for *P. vitticeps* data when compared with data from other species is surprising. In the light of the discussion above, this might be interpreted as indicating *P. vitticeps* has evolved more recently, and has not developed the intraspecific variation which characterises *P. minor*. *P. vitticeps* might also be less variable because it occupies a narrower range of habitats. These are possible explanations, but the answer is more likely to lie with changes in relative growth of *P. vitticeps* after maturity. Differences in allometry at maturity in *P. vitticeps* are less pronounced

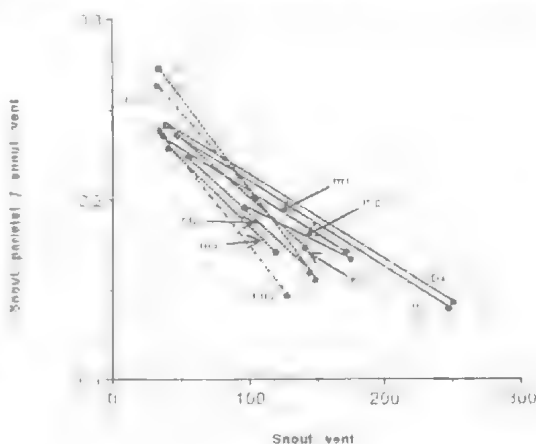


FIG. 7. Snout-parietal data for *Pogona*. Lines and abbreviations as for Fig. 5.

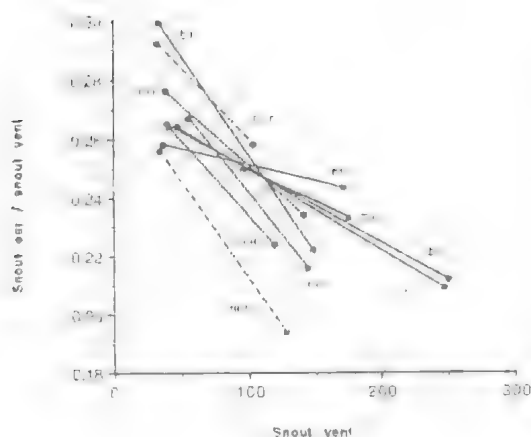


FIG. 8. Snout-ear data for *Pogona*. Lines and abbreviations as for Fig. 5.

than in *P. minor*, allowing a better fit of the calculated curve to the real data (Figs. 1, 2). The *P. vitticeps* data have lower correlation coefficients for measurements where relative growth changes more sharply at maturity, including head width and tail length. In measurements where there is little change in relative growth at maturity, as in hind limb length, the correlations are higher relative to both other measurements and to the data of *P. brevis*.

DISCUSSION

Previous publications using morphometric data of agamids have not included an analysis of growth before and after sexual maturity. The analysis done here comparing these features of growth in *P. minor* and *P. vitticeps* indicate it is a potentially valuable method. However, differences in relative growth after sexual maturity need to be treated with some caution. There is the very real possibility that the recorded differences reflect a 'relative growth' equation derived from different sized adults, rather than sexually mature adults which were still growing. This 'relative growth' would thus be more similar to mammals than most reptiles. In mammals, determinant growth means that population differences may be analysed to show differences in the adult form. For example, deer antlers become relatively larger in large species (Gould, 1977). *Pogona* may have a growth pattern approaching determinant growth. Four adult male *P. brevis* were measured twice, first in October 1990 and again in July 1991. They varied in size from 123 to

147mm snout-vent length on the first occasion, and from 128 to 148 on the second. These animals were mature for some time before their first measurement, so variation in adult size may not indicate age. The data for *P. vitticeps* were certainly affected by differing adult size, as they include measurements from both the small southern form as well as the more widespread 'giant' form (Witten & Coventry, 1990). To gather data free of this problem would require measuring the same animals as they grew to full adult size. There would then be the further complicating factor of determining when sexual maturity had been reached.

Whether or not differing adult size was due to growth after maturity or a longer juvenile growth phase, some sexual dimorphism is apparent from the data presented here. Males have larger heads, indicated by several measurements. Male *Pogona* may engage in physical territorial contests (pers. obs.), apart from displays such as head-bobbing. It would be interesting to investigate whether increased head size in males led to increased reproductive success, and whether this was related to physical encounters or ritualistic displays. Sexual dimorphism in snakes is closely correlated to the presence of male combat, with species exhibiting male combat having larger males (Shine, 1994). There is some variation in male behaviour within Australian agamids. Males of *Amphibolurus nobbi* (Witten, 1974) and *Ctenophorus fordii* (Cogger, 1978) apparently lack territorial behaviour, and the presence or absence of similar dimorphism in those species would therefore be of interest.

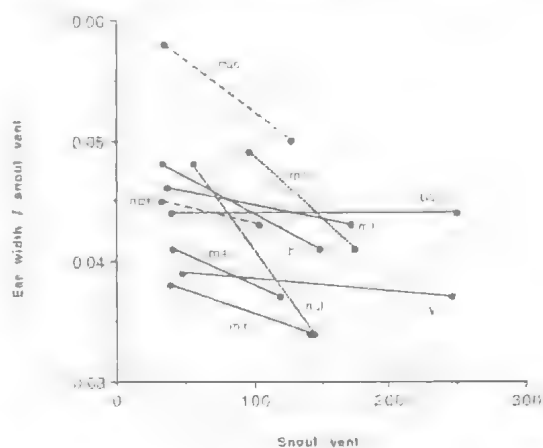


FIG. 9. Ear width data for *Pogona*. Lines and abbreviations as for Fig. 5.

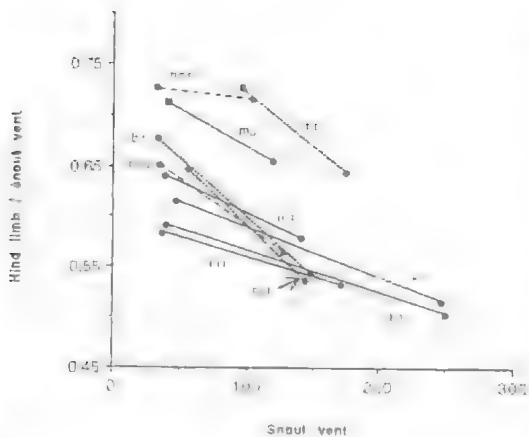


FIG. 10. Hind limb length data for *Pogona*. Lines and abbreviations as for Fig. 5.

The differences observed between the sexes do suggest that any differences between the sexes ideally should be minimised or eliminated before making interspecific comparisons. However, there is little difference in limb proportions between the sexes of the two species with adequate data, nor are there large shifts in allometric rates of change at sexual maturity for these features (Fig. 3). While there is no guarantee that this holds for the other species studied, it is likely that interspecific differences recorded in these measurements are not greatly affected by sexual dimorphism.

It should be pointed out that the methods used here to illustrate morphometric differences were deliberately chosen to highlight small differences. The data presented by Witten (1985) came from a much wider group of lizards, and many species analysed there would be off the scale of the figures presented in this paper. The data presented there were used to illustrate broad differences between species of different genera, often adapted to very different niches. However, morphometric data are useful in analysing differences even subspecies.

The variation within *P. minor* is remarkable. In head size in general, and head width in particular, *P. m. mitchelli* is less similar to the type species than *P. vitticeps*, so named because of its wide head. This remarkable diversity of form fits within the one breeding population, as there is little doubt that these subspecies intergrade in the north west of Western Australia (Storr, 1982; Witten, 1994).

The intraspecific differences within *P. minor* are similar to those between other species of the genus. One aspect of this variation is that *P. m. minima*, from islands off the West Australian coast, is quite different morphometrically to otherwise similar specimens from the adjacent mainland. Badham (1976) placed mainland specimens in the species *minima*, which Storr (1982) reduced to a subspecies of *P. minor*, and restricted to specimens from the Houtman Abrolhos Islands. Morphometric data support Storr's position. There is a morphological cline from east to west in mainland *P. m. minor* with far western specimens very similar to *P. m. minima* (Witten, 1994). It seems the continued gene flow between mainland populations has had the effect of preventing major changes in body proportions. The interruption in gene flow by marine barriers has apparently allowed *P. m. minima* to differentiate morphometrically.

The maintenance of a cline within *P. minor* appears to be the result of different selective pressures operating within the range of the species. Animals from the south west are apparently evolving toward the more arboreal habitat preference of the *Amphibolurus* radiation, while those of central Australia resemble other species of *Pogona* from arid habitats (Witten, 1994). The mainland population clearly interbreeds, maintaining gene flow between the arid- and mesic-adapted morphs. However, gene flow between *P. m. minima* and the mainland populations has clearly been interrupted by rising sea levels. The effect of a recent interruption to continued gene flow on morphometric evolution is

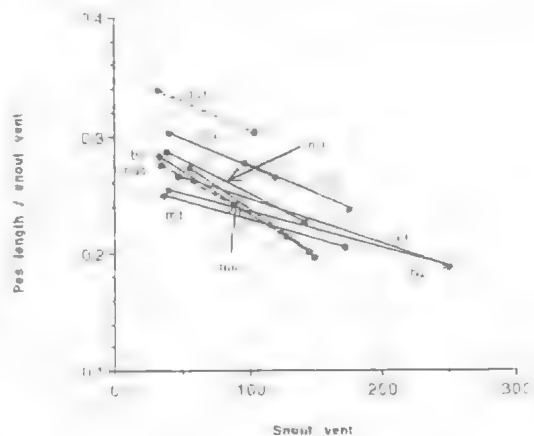


FIG. 11. Pes length data for *Pogona*. Lines and abbreviations as for Fig. 5.

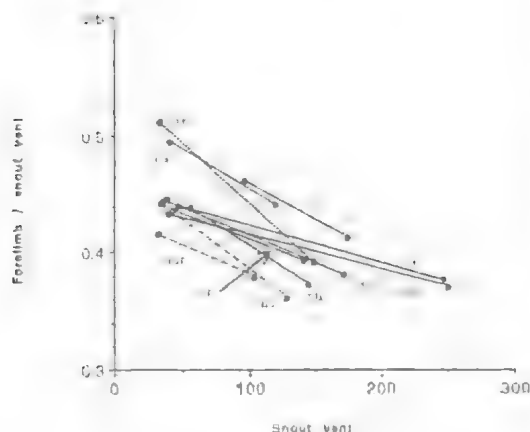


FIG. 12. Forelimb length data for *Pogona*. Lines and abbreviations as for Fig. 5.

remarkable. All mainland *P. minor* retain very similar juvenile proportions (Figs 3, 4), even when there are marked differences as adults, such as in head width (Fig. 3). *P. m. minima* appears to have been freed from this early conservatism, as it differs in a number of proportions throughout growth, but particularly in tail and limb lengths (Fig. 4). There are possible explanations apart from interruption to gene flow, but this is the most obvious factor relevant to the situation.

Variation within *P. minor* is of interest from several perspectives. Witten (1985) suggested morphometric differences were of sufficient phylogenetic importance to base genera on them. While the differences within *P. minor* are not of the same magnitude observed between different genera, they are significant, and cast doubt on the presumed conservative nature of such characters. If significant differences occur within populations of one species, this may indicate an ability to quickly evolve significantly different allometric features. Other data, however, point to a long maintenance of variation within *P. minor*. *P. m. minima* shares morphological features with both *Chlamydosaurus* and members of the *Amphibolurus* radiation, and it is probable that these taxa share a common ancestor (Witten, 1994). On this basis, it seems likely that variation within one species has persisted while other descendants from the original population have radiated out to form several new genera, and a large number of species. If this is true the morphometric variation within *P. minor* is less surprising.

Witten (1985) compared morphometric data from only *P. barbata* and *P. vitticeps*. The choice

of these two species from the perspective of variation within the genus was unfortunate, as they are very similar in most measurements. This similarity does not appear to indicate a close phylogenetic relationship, as *P. barbata* is clearly nearer *P. nullarbor*, and *P. vitticeps* is near *P. minor* (Badham, 1976; Witten, 1994). It could be that the large size attained by these species places constraints on the relative proportions of the animals, in the way hypothesised by Dodson (1975). In support of this idea, the next largest species of the genus, *P. microlepidota*, is also similar to the two giant species in several measurements, although not all.

P. brevis differs from other species in many of its juvenile proportions (see especially Figs 6-8). This is contrary to the expectations of Gould (1977), who predicted more similarity in closely related taxa, and to the findings of Witten (1985) who demonstrated more similarity in juvenile proportions than in other morphometric data of agamids. The data for *P. brevis*, however, differs somewhat from those of other species, in that there were a number of very small individuals, down to 33mm snout-vent length. In other species few small specimens were examined, and none as small as the smallest *P. brevis*. The steep changes in ratios during early growth may produce large differences in the calculated measurements for the smallest *P. brevis*. The apparent differences between the smallest *P. brevis* and other species is more likely to be the result of using data from very small specimens than any large difference in juvenile proportions.

Morphometric data from *Amphibolurus norrisi* and *Ctenophorus nuchalis* were compared with data from

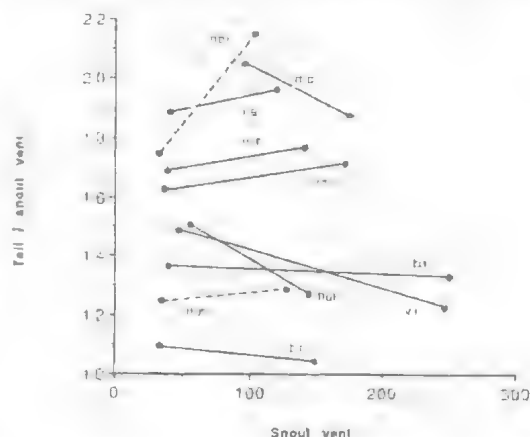


FIG. 13. Tail length data for *Pogona*. Lines and abbreviations as for Fig. 5.

Pogona. It is clear from morphological data that the former has derived from an animal resembling *P. minor* (Witten, 1994), and the latter shares some derived features with *Pogona*, and may be similar to its ancestor (Witten, 1982). Morphometric data are consistent with these hypotheses. In most features there is at least one taxon within *Pogona* which closely resembles one or other of these species. *Ctenophorus nuchalis* and its relatives differ from other *Ctenophorus* species groups in possessing a short blunt head, and very short limbs (Witten, 1985). These features are very similar in *P. brevis* and *P. nullarbor*, more so than other members of the genus. It is interesting to speculate that this indicates these species are more primitive within the genus. A distinctly longer tail has evolved in *P. minor* and *P. microlepidota*, a feature shared with *Amphibolurus*. This may represent a derived character within *Pogona*, and indicate a relationship to *Amphibolurus*. However, this should be considered speculative. Selective pressures may shift body proportions quite rapidly, if the differences in *P. m. minima* are taken as an indication. The conservation of body proportions in mainland *P. minor* is probably the result of continuing gene flow from a large arid-adapted population to a comparatively small mesic-adapted population rather than any innate conservatism. Morphometric analyses usually support relationships inferred from other data, however, and may be useful where other such data are lacking.

ACKNOWLEDGEMENTS

By breeding *Pogona brevis* Jon Birkett of the Melbourne Zoo both inspired and made possible parts of this study. I thank him and his staff for their cheerful cooperation and assistance. Specimens were borrowed from the Queensland Museum, Australian Museum, Museum of Victoria, South Australian Museum and the Western Australian Museum. My thanks to J. Covacevich, P. Couper, R. Sadler, J. Coventry, M. Hutchinson and L. Smith for the loan of this material.

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APPENDIX

Specimens examined:

Pogona barbata: AMR17904, AMR20987, AMR21578, AMR25789, AMR59988-90, AMR59992, AMR107397, AMR107399-405, AMR107407-8, AMR107411-3; QMJ49966; NMVD137, NMVD151, NMVD723, NMVD744, NMVD896, NMVD966, NMVD1345, NMVD7934, NMVD8038, NMVD14034, NMVD14036, NMVD14679, NMVD14699, NMVD48900, NMVD57127.

Pogona brevis: AM field series 11238, 11240; QMJ32292, QMJ38735, QMJ38760-2, QMJ46949; NMVD11164-5; WAMR9856.

Pogona microlepidota: WAMR43028, WAMR44258, WAMR46847, WAMR46962, WAMR56232, WAMR57108.

Pogona minor minor: AMR15182, AMR5660-1, AMR7658; NMVD493, NMVD2657, NMVD2979, NMVD3010, NMVD3037, NMVD3052, NMVD65339, NMVD65361, NMVD65379; SAMR322, SAMR587, SAMR1402A-D, SAMR4820, SAMR5312, SAMR6556, SAMR9520, SAMR14482, SAMR14635, SAMR14955A-C, SAMR14986A-C, SAMR15004A-D, SAMR15304, SAMR15506, SAMR15568-9, SAMR18132-3, SAMR18168-9, SAMR18376, SAMR21374, SAMR22914-5, SAMR24479, SAMR25427-8, SAMR25673, SAMR26389, SAMR26809, SAMR28437, SAMR28525, SAMR29903, SAMR30083, SAMR31872, SAMR31875, SAMR31916, SAMR31923, SAMR31939-40, SAMR31961, SAMR31989, SAMR32011, SAMR32019, SAMR32036-8, SAMR32073, SAMR32076, SAMR32095, SAMR32142, SAMR32146, SAMR32165, SAMR32174, SAMR32189, SAMR32205, SAMR32214, SAMR32218, SAMR32279, SAMR32288, SAMR32312, SAMR32613, SAMR32622, SAMR33983, SAMR36226, SAMR37656; WAMR19568, WAMR31004, WAMR34182, WAMR34197-8, WAMR45206, WAMR46634-5.

Pogona minor 'minima' morphs: AMR133759, AMR133915, AMR133988, AMR136236, AMR136239; NMVD772-4, NMVD2435, NMVD8002; SAMR22836; WAMR23812, WAMR37737, WAMR87461.

Pogona minor minima: WAMR19501-16.

Pogona minor mitchelli: AMR38712, AMR100912-5, AMR101470-1, AMR101550; SAMR1399-1400, SAMR1404, SAMR3436, SAMR3546, SAMR15622; NMVD999-1001; WAMR13066, WAMR15823, WAMR19377, WAMR45758-60, WAMR46068, WAMR50696, WAMR68983, WAMR79111-2, WAMR87344.

Pogona nullarbor: SAMR5034, SAMR5437, SAMR14313A-B, SAMR14314, SAMR15570, SAMR18170, SAMR19807, SAMR20106, SAMR22290, SAMR23005, SAMR23029, SAMR23939-41, SAMR25298-301, SAMR26171, SAMR26393, SAMR26395; WAMR16888, WAMR16896, WAMR24655, WAMR28127, WAMR31964-5, WAMR91743, WAMR91831-2, WAMR91870, WAMR91924.

Pogona vitticeps: AM field series 11252; AMR13904-5, AMR15296, AMR17122-3, AMR21077, AMR47319, AMR59991, AMR59996-7, AMR107398, AMR107406, AMR107409-10, AMR107444; NMVD648, NMVD699-700, NMVD777, NMVD787, NMVD970, NMVD1031, NMVD1036, NMVD1123, NMVD3072, NMVD7871, NMVD8970, NMVD11753-4, NMVD12164, NMVD14181, NMVD15379, NMVD15382, NMVD18220, NMVD41501-2, NMVD47858, NMVD52088-9, NMVD52637, NMVD52742, NMVD53482, NMVD53827, NMVD53836, NMVD53853, NMVD53907, NMVD53925, NMVD54051, NMVD54070-1, NMVD54123, NMVD54131-2, NMVD54144, NMVD54557, NMVD54749, NMVD54754, NMVD54759-60, NMVD54789-90, NMVD55036, NMVD55064, NMVD55251, NMVD55305, NMVD55583, NMVD56741, NMVD58472, NMVD58477, NMVD58501, NMVD58548, NMVD58555, NMVD58570, NMVD59448, NMVD59818, NMVD60324-5, NMVD60609, NMVD60694-5, NMVD60708, NMVD60741, NMVD60760, NMVD60762-3, NMVD60768-9, NMVD60778, NMVD60785, NMVD60826-8, NMVD60841, NMVD60854, NMVR4547-8, NMVR4855, NMVR13781-2.

Ctenophorus nuchalis: AM field series 11228, 11327, 11329-31; AMR542, AMR2113-4, AMR4892, AMR7024, AMR9540, AMR10873-5, AMR11924, AMR11928-30, AMR11936, AMR11938, AMR11943, AMR11946, AMR11954-5, AMR11981, AMR11983, AMR13911-3, AMR13918, AMR13920, AMR13925, AMR17260, AMR17610, AMR21466-9, AMR107377-81.

Amphibolurus norrisi: NMVD14804-5, NMVD51499, NMVD51507, NMVD51576, NMVD51608, NMVD51617, NMVD51729, NMVD51752, NMVD51759, NMVD51763, NMVD51765, NMVD51771, NMVD52550, NMVD52557, NMVD52562, NMVD52632, NMVD52677, NMVD52693, NMVD52996, NMVD53057, NMVD53072, NMVD53077, NMVD53470, NMVD53488, NMVD53501, NMVD53854-5, NMVD53916, NMVD54119, NMVD54150, NMVD54152, NMVD54154, NMVD54202, NMVD55606.

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